The Samoan Land Snail Genus *Ostodes*

(Mollusca : Prosobranchia : Poteriidae)

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I. INTRODUCTION

THIS REPORT IS MODIFIED from a dissertation submitted in 1973, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, to the Graduate School of Northwestern University, Evanston, Illinois. It revises the species of the land snail genus *Ostodes* Gould, 1862, which is found only in Western Samoa and American Samoa. Three new species, *Ostodes **reticulatus**, O. **exasperatus**,* and *O. **llanero**,* are described, and the previously compound species *O. plicatus* (Gould, 1848) is redefined. Investigation showed that there are species recognition differences in terminal structures of the genitalia. While the presence of such differences is well known in pulmonate land snails, this is, to my knowledge, the first report of this phenomenon in land prosobranchs.

The work is based upon materials in the mollusk collection of the Field Museum of Natural History, Chicago. The methodology used required having shells and soft parts associated at the start of data capture. Material in the Museum of Comparative Zoology, Harvard University, and Bernice P. Bishop Museum is stored with the shells in one cabinet and the soft parts in another; therefore loans of anatomical materials from those institutions were not requested.

In the absence of personal field work, no information on niche differentiation can be presented. Some data on the anatomy of extralimital Pacific island taxa and one Neotropical taxon are presented for establishing outgroup comparisons.

The members of my committee, Dr. Frank A. Brown, Jr., Dr. Olin Rulon, and Dr. Alan Solem have given advice and counsel, and have been most patient with a very protracted period of study. Drs. Kenneth J. Boss, of the Museum of Comparative Zoology, Harvard University; Frank Climo, Dominion Museum, Wellington, New Zealand; Joseph Rosewater, United States National Museum; Bertram Woodland and Carol Jones, Field Museum of Natural History; Shi-Kuei Wu, University of Colorado, Boulder; and Frederick Schramm, Eastern Illinois University, Charleton, loaned specimens or gave advice. Dr. Winston Ponder, Australian Museum, Sydney, allowed me to examine the holotype of *Cyclostoma brazieri* Cox, 1870.

Mrs. Carole W. Christman bore patiently with my inexperienced dissections, and taught me a great deal in the process of producing the illustrations. Her artistic skill was available through the generosity of my father, Frederick K. Leisch, whose timely gift to the Field Museum was used in part to support Mrs. Christman's work. Mr. Fred Huysmans and Mr. John Bayalis of Field Museum of Natural History prepared the photographic prints used in this paper. Elizabeth Liebman drew some of the quantitative diagrams.

I am indebted to Dr. Solem for the SEM photographs of the radulae, to Dorothy Karall and Claire Kryczka for mounting figures, and to Jayne Freshour for manuscript typing. Miss Evelyn Patterson and Mr. Vic Snodgrass helped with translations from the Latin. Barbara Walden assisted in labeling figures and cataloguing.

Finally, I wish to thank my husband, Joseph B. Girardi, who refused to let me quit when I got discouraged, helped with German translations, and put up with sloppy housewifery while I studied; and my daughters, Stephanie and Susan, who bore cheerfully with their part-time mother.

II. HISTORICAL REVIEW OF CYCLOPHORID CLASSIFICATION

The family Cyclophoridae was first established by Gray (1847: 181–182). It included a miscellany of genera previously included in Cyclostomacea of earlier authors such as Anton (1839: 52–54). Over the next few years, additional genera were added by various authors, the placement being based entirely on shell characters. Pfeiffer (1852: 14) formally grouped the Cyclophoridae and the Pomatiasidae into the superfamily Cyclostomacea. He divided the Cyclophoridae into 4 groups that were roughly equivalent to modern subfamilies, which he named Cyclotea, Diplommatinea, Cyclophorea, and Pupinea. Fischer (1885: 739) separated the Cyclophoridae from the Cyclostomatidae on animal and radular characters.

Kobelt (1902: 336, 484, 231) recognized 3 additional subfamilies – Alycaeinae, Craspedopomatinae, and Neocyclotinae, giving great importance to zoogeographic factors. Thiele (1929: 94–113) essentially utilized Kobelt's system.

The first substantial innovation was by Tielecke (1940). His work was based on consideration of male and female reproductive systems, central nervous system, and organs in the pallial cavity, particularly the kidney and circulatory system. He felt strongly that anatomical differences were more fundamental than similarities in shell and radular characters, and that Thiele's system was artificial. On the basis of his findings he re-grouped the cyclophorids into a superfamily with 5 families: Cyclophoridae (with 2 subfamilies); Maizaniidae (which Thiele, 1929, had considered to be a subgenus of *Ostodes*); Poteriidae (with all the New World and Pacific Island helicoid tropical genera, including *Ostodes*); Pupinidae (with 2 subfamilies); and Cochlostomatidae, also with 2 subfamilies. Because he derived information from 3 separate organ-systems, Tielecke's work is the most extensive and the soundest yet done on this group.

Torre, Bartsch, & Morrison (1942) used only shell and opercular characters in classifying the American Cyclophoridae into 4 subfamilies: Megalomastominae (elongate shells with corneous operculum); Diplommatininae (pupoidal shell); Amphicyclotinae (helicoid shells with corneous operculum); and Aperostominae (helicoid shells with calcareous operculum).

Morrison (1955) described the external male reproductive systems of several American cyclophorids, and grouped all the genera into 2 families: the Amphicyclotidae with an enclosed, tubular vas deferens; and the Neocyclotidae, with an open seminal groove ascending the penis.

Thompson (1967, 1969) used the concept of a single large family, Cyclophoridae, recognizing the subfamilies Megalomastominae, Neocyclotinae, and Crocidopominae in Neotropical taxa, based on several characters in both male and female reproductive anatomy.

My own work has been mostly at the species level. I agree with Solem (1959: 182 and unpublished MS.) that the change from open seminal groove to closed vas deferens is by itself insufficient grounds for separation of families. I accept Tielecke's system and consider the cyclophorids as a superfamily containing 5 families, as follows (Tielecke, 1940: 365, 366): Cyclophoridae, with

subfamilies Cyclophorinae and Spirostomatinae; Maizaniidae; Poteriidae; Pupinidae, with subfamilies Pupinellinae and Pupininae; and Cochlostomatidae, with subfamilies Diplommatininae and Cochlostomatinae.

The family Poteriidae has representatives in Central America, South America, the West Indies and the South Pacific. It is characterized anatomically in the male by the location of the penis on the dorsal mid-line of the head, behind the tentacles, while in the female the oviduct, seminal receptacle, and bursa copulatrix all enter the uterus via a common genital duct. Tielecke dissected four of the genera: *Poteria* Gray, 1850, from Jamaica; *Amphicyclotus* Crosse & Fischer, 1879, from Central America; *Aperostoma* Troschel, 1847 (as *Cyrtotoma* Mörch, 1852) from Mexico; and *Ostodes* Gould, 1862 from Samoa. Thompson (1967, 1969) has dissected additional taxa, although coming to very different systematic conclusions.

III. PREVIOUS STUDIES OF THE GENUS *Ostodes*

Early work was purely descriptive, as expeditions and traders brought back material for study. The 1840's to 1870's were the height of land snail descriptive work, with full-time efforts devoted simply to naming the flood of new materials. Because the association of some names with actual populations has presented problems, detailed itemization of early descriptions is necessary.

Between 1838 and 1842, the United States Exploring Expedition, under the command of Charles Wilkes, visited various South Pacific Islands, including Upolu, Western Samoa. Shells were collected principally by J. P. Couthouy, assisted by C. D. Pickering (anthropologist), Joseph Drayton (artist), and W. D. Brackenridge (botanist). Upon the Expedition's return, the mollusk collection was shunted from one depository to another, badly mishandled, and finally turned over (in part) to Augustus A. Gould for study and description (Johnson, 1964: 6–11). Gould read his descriptions of *Cyclostoma tiara, C. strigatum,* and *C. plicatum* in 1847. His descriptions were published the following year (Gould, 1848), and subsequently expanded in the text of the U. S. Exploring Expedition (Gould, 1852). The Expedition's Atlas of Shells finally appeared several years later (Gould, 1860), with the three species of *Ostodes* illustrated on plate 8.

Recluz (1851: 213; plt. 6, figs. 10, 11) described and figured *Cyclostoma apiae,* collected by M. Charbonnier, from Apia, Upolu. Pfeiffer (1854: 301–302; plt. 40, figs. 13, 14) described and figured *Cyclostoma pulverulentum* from Upolu, and in the same year Hombron & Jacquinot (1854: 50, plt. 12, figs. 25–28) described and figured *Cyclostoma albida* from Samoa, without further locality. Souverbie (1858: 294; plt. 8, fig. 6) published a description and illustration of *Cyclostoma gassiesi* from an unknown locality.

Gould (1862: 283) proposed the generic name *Ostodes* for the group of 7 Samoan species previously included in Pfeiffer's *Cyclophorus,* section 6. The cited differences of these 7 species from those remaining in *Cyclophorus* were the elongated shell form, simple aperture, deep, spiral umbilicus, and closer resemblance to the assimineid genus *Omphalotropis.*

Mousson (1865: 180) described *Cyclophorus upolensis,* collected on Upolu by M. Graeffe. Four years later the same author (Mousson, 1869: 351; plt. 14, fig. 9) described *Cyclophorus (Ostodes) adjunctus* from Tutuila, Samoa. Cox (1870: 85) described *Cyclostoma brazieri,* collected by Brazier from under decaying logs on the mountains of Upolu, Navigator's Islands (Samoa). I have examined the holotype of *C. brazieri,* (Australian Museum C64837) and find it to be definitely not an *Ostodes,* nor even a poteriid; it probably belongs to the Assimineidae.

Garrett (1887: 124–153) published the only geographical survey of Samoan land snails, drawing on his own experiences and collections in the field.

Kobelt (1902: 153) summarized the genus and listed 16 Polynesian species. Thiele (1929: 99) combined *Ostodes* with an African genus, *Maizania,* and figured a radula from the latter group.

Only one of the above authors gave data on other than shell, operculum, and radula. Gould (1852: 103) reported that the animal of *Ostodes plicatus* had a long muzzle like a proboscis, long tapering tentacles, and distinct eyes. Its foot was "pale ochreous, upper part of head, neck, and sides a faint red."

Tielecke (1940) examined the anatomy, at least in part, of cyclophorids belonging to 44 species and 19 genera. Most of the material came from the Sunda-Archipel Expedition of Dr. Rensch, and some from the collection of Dr. Degner in the Zoologisches Museum, Hamburg. Specimens identified as *Ostodes strigatus* were available from Apia, Upolu. Their true identity is uncertain, since *O. strigatus,* although originally described from Upolu, is now known only from Tutuila, American Samoa. Tielecke examined the male and female reproductive tracts, the central nervous system, and the pallial cavity, particularly in reference to the kidney and circulatory system.

Clench (1949: 4–29) revised the Pacific Island cyclophorids in the collection of the Bernice P. Bishop Museum, Honolulu. He worked only with shell, operculum, and radula, and did not study the soft anatomy. Clench described and figured 3 new species (*Ostodes cookei, O. savaii,* and *O. garretti*), and refigured 5 previously known

species. Earlier authors, such as Pease (1871: 475), had synonymized *O. plicatus* and *O. strigatus,* but Clench (1949: 14) stated that they were distinct and that Gould "was in error in assigning this species [*O. strigatus*] to Upolu rather than to Tutuila." Clench synonymized *Cyclostoma gassiesi* with *Ostodes plicatus.* I have seen some of the material studied by Clench. Of the 15 shells in one lot identified as *O. plicatus* (MCZ 140507), two are *O. plicatus,* the rest are *O. gassiesi.* Since anatomical data led to my recognition of their distinctness, this confusion could only be expected. From extralimital areas, Clench described a number of species and genera. These are mentioned in the section below on other Pacific Island poteriid genera.

IV. MATERIAL STUDIED

Most of this study was based on some 900 live-collected snails in the collection of Field Museum of Natural History, Chicago (hereafter FMNH). These specimens were collected on Upolu and Savaii, Western Samoa, by Dr. Alan Solem and Mr. Laurie Price in October through December 1965, and by Mr. Price on Tutuila in March and April 1975. This field work was supported by National Science Foundation Grant GB-6779 to the Field Museum in support of research by Dr. Solem, and by Office of Endangered Species contract 14-16-0008-873 to Field Museum to survey endangered land snails of American Samoa. The animals had been drowned in water to which chloral hydrate had been added as a relaxant, and then preserved in 70% ethyl alcohol. Shells and soft parts were stored together.

Specimens of poteriids from New Caledonia and the New Hebrides in the Field Museum collection were dissected for comparative purposes, as were specimens of *Mexcyclotus panamensis,* from Panama. The latter are figured for outgroup comparison.

Some shell material was borrowed from the Museum of Comparative Zoology (hereafter MCZ), Harvard University, and from the United States National Museum (hereafter USNM), Washington, to check on published identifications and to verify some of my own identifications.

V. METHODS

For each specimen whose sex could be determined, 10 shell parameters were recorded. Height, diameter, umbilical width, and horizontal diameter of the aperture were measured with a vernier caliper or (for very small specimens) an ocular micrometer. Whorl count, and both dorsal and ventral sculptural elements were counted with a binocular microscope at 10X magnification, spire angle was estimated by holding the shell against a printed protractor, and thickness of the parietal callus was estimated on a scale of one to three (one indicating a very thin callus, and three indicating a parietal callus as thick as the outer rim of the aperture). The character of the umbilical margin was scored as being smoothly rounded, sharply angled, or bordered by a rim composed of the innermost ventral spiral lira. Ratios of shell height to diameter, and of shell diameter to umbilical width were calculated for each specimen.

Empty shells, and snails that had been so severely contracted during preservation that they could not be extracted for sexing, were not measured in detail. Where many specimens in a lot were severely contracted, some shells were broken after measurement to allow sexing.

Specimens were accepted as adult that had started a changed pattern in growth, indicated by the following 3 features: (1) thickening of the parietal callus; (2) a change in the sculptural pattern on the terminal portion of the body whorl; and (3) an increase in the rate of decoiling resulting in the last portion of the body whorl being inset under the periphery of the penultimate whorl. In many snails the onset of reproductive activity is marked by just these alterations in growth patterns, when the energy budget of the individual shifts from individual growth to production of the next generation. Characteristic external genital features of both male and female *Ostodes* develop while the shell is still very small, although the internal reproductive systems remain small and undeveloped. Neither material nor time was available for determining exactly when sperm and egg production begins; much larger samples, preserved for histological examination, would be required to establish the degree of correlation between shell growth changes and onset of reproductive activity. In the absence of such material, specimens showing the growth changes were classed as mature, while those without the changes were considered juvenile. Only adult shells are cited in the species diagnoses, and means and standard deviations of populations are based on adult materials only.

For males, the penis was measured with an ocular micrometer, the lengths of the thick proximal trunk and the tapering distal thread were recorded, and the ratio of thread to trunk was calculated. For female snails, shapes and orientations of anus and vaginal orifice profiles were noted.

Internal reproductive anatomy was studied by dissecting, where possible, at least three males and three females of each species. Drawings were rendered by close collaboration of artist and investigator, with the specimen being

dissected in progressive stages so that the artist could depict internal structures and fine details. The method of preservation used precluded histological studies.

Opercula were removed and studied for approximately 25% of the specimens. Examples of each opercular type were studied with both ordinary and polarized light, then embedded in paraffin and sectioned. The presence of calcium deposit was tested for with dilute HCl.

Radulae of *Ostodes gassiesi*, *O. reticulatus*, *O. plicatus* and *O. llanero*, as well as *Gonatorhaphe* sp. and *Gassiesia* sp., were prepared and photographed by Dr. Alan Solem with a scanning electron microscope as part of a cooperative research program between Field Museum of Natural History and the American Dental Association. Preparation technique was that of Solem (1972).

VI. SYSTEMATIC REVIEW

A. Variations in Structural Features

The basic systems used in species separation and classification are: (1) the shell; (2) the operculum; (3) the radula; and (4) the gross anatomy. The patterns of variation within *Ostodes* are here reviewed in order of their initial use in systematics.

1. SHELL FORM AND ORNAMENTATION

The basic shell form in *Ostodes* is turbinate. The form varies from species to species, with *O. gassiesi* and *O. plicatus* adults being narrowly turbinate (taller than wide), *O. savaii* being of approximately equal height and width, and the other species being more or less broadly turbinate, with *O. garretti* having the least elevation of the spire. Juveniles of all species, even *O. gassiesi* and *O. plicatus*, are broadly turbinate, wider than high (Figure 1).

The periphery of the body whorl in *Ostodes tiara*, *O. garretti*, *O. adjunctus*, and the "smooth" form of *O. upolensis* varies from moderately to sharply carinate. Adults of all the other species have round-shouldered body whorls, even when the early whorls were carinate.

Ostodes gassiesi, *O. plicatus*, *O. savaii*, *O. tiara*, and *O. garretti* have deep, narrow umbilici (mean D/U ratio 3.31). *O. strigatus*, *O. exasperatus*, *O. reticulatus*, *O. adjunctus*, *O. upolensis*, and *O. llanero* have wide open umbilici, with a mean D/U ratio of 2.76. The width of the umbilicus is affected by 2 factors: the rate of whorl translation (rate of decoiling) and the size of the generating curve, as measured by the diameter of the aperture (Raup & Stanley, 1971: 158). In two species with equal-sized apertures, that which decoils faster will have the smaller umbilicus. In two species with equal rates of whorl translation, the one with the larger generating curve will have the smaller umbilicus. Of the 2 factors, the rate of decoiling has the greater influence in *Ostodes*. Table 1 shows

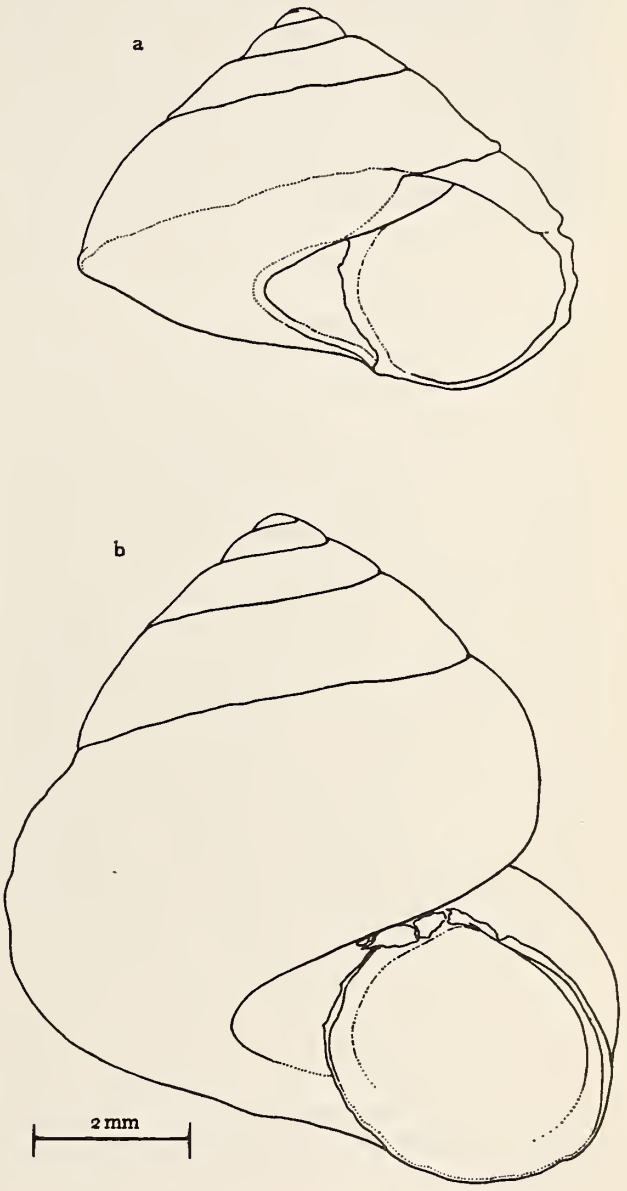


Figure 1

Shell outlines of *Ostodes gassiesi*

a – juvenile b – adult

the species of *Ostodes* arranged, from the top down, in order of increasing size of umbilicus: *O. gassiesi* with the smallest umbilicus at the top, *O. llanero* and the "stepped" form of *O. upolensis* at the bottom. (Table 1 compares juveniles of *O. llanero* with adults of the other species; Figure 23 compares the same specimens of *O. llanero* with juveniles of the other species. The relative position of *O. llanero* with respect to the other species is the same. It therefore seems reasonable to assume that, if adults of *O. llanero* had been available for examination, they would still have fallen at the bottom of Table 1.) This arrangement also puts the species generally in order of rate of decoiling, fastest at the top and slowest at the bottom, and in approximate order of size of aperture, largest at the top, smallest at the bottom. If the data for pairs of similar species, such as *O. tiara* and *O. garretti,* or *O. savaii* and *O. exasperatus,* be compared, it will be seen that that species of the pair which decoils faster will have a smaller umbilicus and usually also a larger aperture.

The pair for which the above statement does not hold true is the 2 forms of *Ostodes upolensis.* The stepped form decoils much faster than the smooth form (Figure 24) and should therefore logically have a smaller umbilicus. Instead, its umbilicus is larger than that of the smooth form, which would lead one to suspect it must therefore have a much smaller aperture. Not so; the stepped form has a larger aperture than the smooth form. The reasons for this apparent violation of the rules governing shell morphology can be seen in the silhouette of the smooth form (Figure 24b). Unlike most other species of *Ostodes* and the stepped form of *O. upolensis,* this form retains a pronounced peripheral carina which persists into adulthood. The carina protrudes sideways and increases the diameter of the shell in proportion to its umbilicus. Also, the inset of the terminal portion of the body whorl under the penultimate whorl is proportionally much greater in the smooth form of *O. upolensis* than in the other species of *Ostodes,* so that the umbilicus is impinged on and made smaller.

The aperture ranges in shape from round to very slightly compressed, and is appressed to the penultimate whorl. The outer apertural lip is simple, with no flange or ornamentation. The thickness of the parietal callus varies with the species and the age of the individual.

The spire and early whorls are smooth in all species of *Ostodes.* Although the smoothness might be due to wear, I think it is more likely the true primary condition of the shell because (a) it is seen even in very small, unworn juveniles and (b) the sculpture shows a distinct pattern of beginning from a smooth surface, as discussed below.

Except for *Ostodes cookei,* which is smooth, *Ostodes* shells are ornamented with spiral lirae, radial plicae, or both, according to the species. All species (except *O. cookei*) have spiral lirae, although they are quite unobtrusive in *O. plicatus.* The first spiral lira begins low down on the whorl, just above the suture, at about the beginning of the third whorl. The second spiral thread starts a little further along the whorl, and a little higher up, and so forth, until the full complement of spiral lirae is present by about the start of the fourth whorl. The spiral lirae are usually evenly distributed on the whorl, except in *O. gassiesi,* where they are clustered on the lower portion. The spirals continue in juvenile shells right up to the aperture; in adults, they fade out a few millimeters

Table 1

Mean Diameters of Umbilicus and Aperture in Relation to Shell Diameter in *Ostodes*

Species	N	D/U	D/A	H/D	Spire angle (°)
Ostodes					
gassiesi	126	3.42 ± .04	2.40 ± .01	1.07 ± .01	80 ± 0.5
tiara	15	3.38 ± .12	2.40 ± .03	0.79 ± .01	107 ± 0.9
plicatus	57	3.37 ± .05	2.37 ± .02	1.06 ± .01	81 ± 1.1
savaii	103	3.18 ± .04	2.43 ± .01	0.98 ± .01	86 ± 0.7
garretti	4	3.18	2.51	0.78	108
adjunctus	17	3.02 ± .09	2.74 ± .05	0.75 ± .01	92 ± 1.9
exasperatus	24	2.98 ± .09	2.51 ± .02	0.92 ± .01	90 ± 1.6
upolensis (smooth)	10	2.91 ± .19	2.61 ± .21	0.76 ± .05	98 ± 4.0
strigatus	84	2.89 ± .02	2.57 ± .01	0.91 ± .01	86 ± 0.8
reticulatus	12	2.78 ± .04	2.55 ± .03	0.93 ± .02	92 ± 1.3
upolensis (stepped)	12	2.37 ± .08	2.55 ± .03	0.78 ± .01	98 ± 2.6
llanero	3	2.37	2.61	0.70	110

before the aperture, at about the point where the body whorl is indented under the penultimate whorl. This probably marks the point at which reproductive maturity is reached. The spirals are continued on the lower palatal surface in *O. reticulatus, O. exasperatus, O. llanero,* and *O. adjunctus.* There may be traces of spirals on the ventral surface in *O. upolensis, O. savaii, O. tiara,* and *O. garretti,* but the lower surface of *O. gassiesi* and *O. strigatus* is almost always smooth, while that of *O. plicatus* shows only radial plicae.

Radial plicae are an important element in the ornamentation of *Ostodes gassiesi* and *O. reticulatus,* and are the major sculptural element of *O. plicatus.* In *O. plicatus* they are close-spaced, moderately broad and in high relief. They continue over the shoulder of the body whorl, across the ventral surface and down into the umbilicus. At the edge of the umbilicus, the radial plicae may sometimes be pinched into an acute angle, but they do not form a true rim around the umbilicus in the same way that a spiral lira would. The radial plicae of *O. gassiesi* are somewhat broader and shallower than those of *O. plicatus*; they hardly ever continue onto the lower palatal surface of the shell. The radial plicae of *O. reticulatus* are somewhat more widely spaced and a little narrower, so that there are definite valleys between them. The crossing of these valleys by the overlying spiral lirae creates the reticulated surface which gives the shell its name; it is particularly noticeable on the ventral surface of the shell. Radial plicae are but poorly defined in *O. strigatus, O. savaii,* and *O. upolensis,* and are absent in *O. exasperatus, O. llanero, O. adjunctus, O. garretti,* and adults of *O. tiara.*

The periostracum in *Ostodes* varies from light yellow to moderately dark brown. It is adherent in *O. gassiesi* and *O. tiara,* but is deciduous in the other species. Possibly the most deciduous periostracum is that of *O. plicatus.*

The color of most *Ostodes* shells is white, off-white or cream-color. The only exceptions are *O. gassiesi, O. adjunctus,* and *O. plicatus,* which (sometimes, half the time, and often, respectively) have pink or red spires. If a pink spire of *O. plicatus* be broken, and the broken edge examined under the microscope, it will be seen that the shell is composed of three layers: the inner and outer layers are a translucent white, but the middle layer is a very intense rose-red to salmon color. It looks pinkish from the outside of the shell because of the white layer covering it. In *O. adjunctus,* the color is deeper and the inner white layer is absent.

Shells of *Ostodes* are subject to wear in varying degrees. The factor of wear is important because a badly worn shell is very difficult to place with certainty within a species, especially if it is empty so that anatomical information is lacking. Of all the *Ostodes, O. reticulatus* and *O. upolensis* seem to show the greatest resistance to wear, while *O. tiara* and *O. garretti* are most apt to be found badly worn. Mousson (1865: 179) says of *O. tiara* that even fresh specimens are almost always badly worn, with not only the periostracum missing, but most of the sculptural elements also gone, so that the shell presents a bony-looking, matte surface. This may reflect space niche differences in microhabitat selection, but no data on this aspect are available.

2. OPERCULA

(Figures 2, 3)

Clench (1949) described the opercula of *Ostodes adjunctus, O. cookei, O. plicatus, O. strigatus, O. tiara,* and *O. upolensis,* and figured but did not describe that of *O. savaii.* He mentioned only one type of operculum for each species. The only differences between species cited were concerned with the degree of central depression and the character of the nucleus.

During this study, 198 *Ostodes* opercula were studied in detail. This sampling consisted of adult examples of both sexes from all species except *O. llanero,* for which only juveniles were available. Although all opercula were found to be circular, corneous, and transparent, there were 6 variations of this pattern. They are:

Type A-1: laminate, thin (Figure 2)

Of fairly uniform thickness throughout except for very thin and fragile outermost edge, which resembles cellophane in texture and transparency. Slight thickening sometimes found just inside this "cellophane edge." No spiral structure can be seen with either ordinary or polarized light. Central portion of operculum often shows inclusions resembling air-bubbles or fragments of mucus. Disconnected fragments of spiral lamellae occasionally seen around outer margin. Thin horizontal layering seen in cross-section. Specimen illustrated, 5.1 mm in diameter.

Type A-2: laminate, thick (Figure 2)

Cross section shows approximately same number of horizontal layers as in type A-1, but each layer is much thicker. Operculum thicker in center and near outer rim than in circum-central area. Upper surface flat or very slightly concave. No spiral structure apparent in central part, which shows inclusions as in type A-1. Three or 4 spiral lamellae may be seen around outer edges. No "cellophane edge." Lower surface shows large central papilla, formed by a dipping-down of the horizontal layers, and

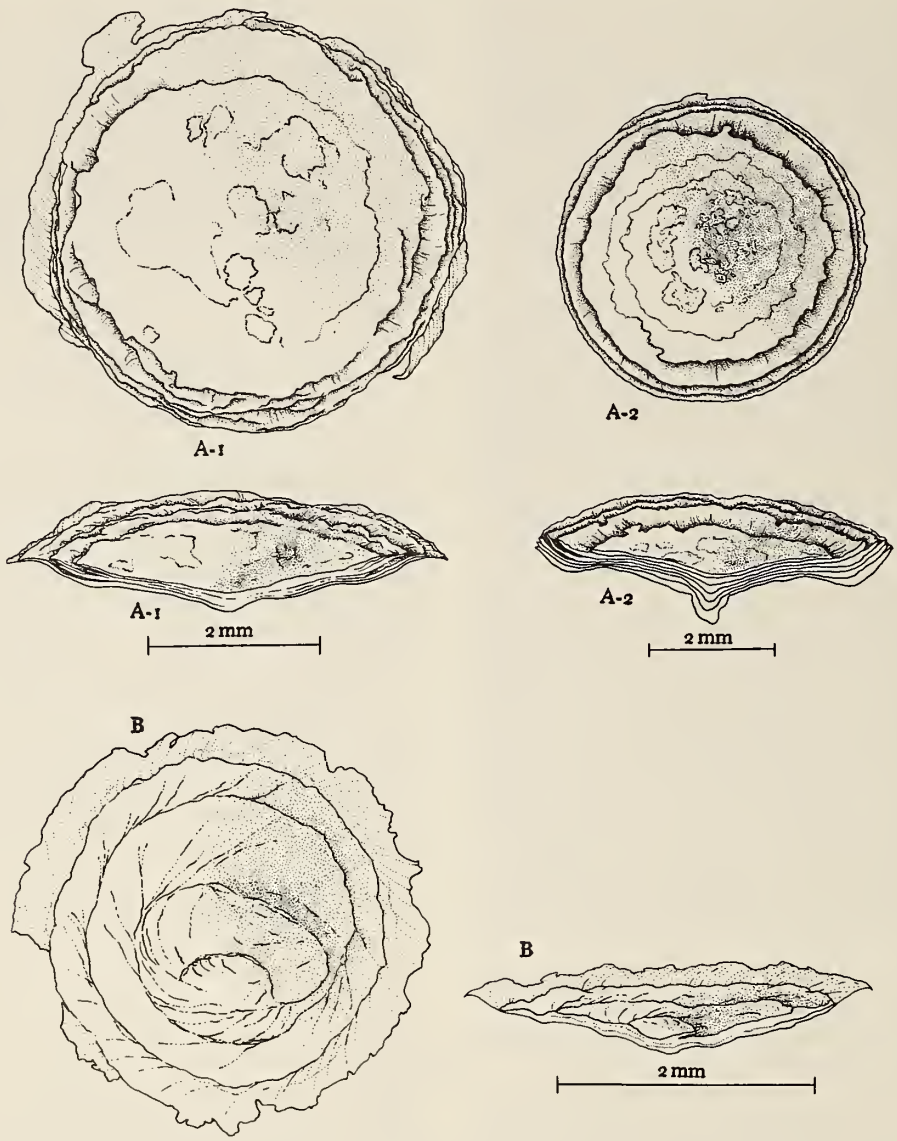


Figure 2

Opercular Types A – 1, A – 2, and B

many faint, fine, closely-spaced radial lines, like brush-marks in wet paint. With transmitted polarized light, many faint, closely-spaced spiral lines can be detected, apparently within the body of the operculum, as they do not show on either surface in any kind of reflected light. Specimen illustrated, 5.9 mm in diameter.

Type B: oligogyrous (Figure 2)

Extremely thin throughout; sometimes flat, sometimes cup-shaped, with flat central portion and edges turned up all around; in *Ostodes strigatus,* may be so acutely concave as to approach a cone-shape. Few (3 – 5) broad, irregular spirals from center to edge. Nucleus often somewhat off-

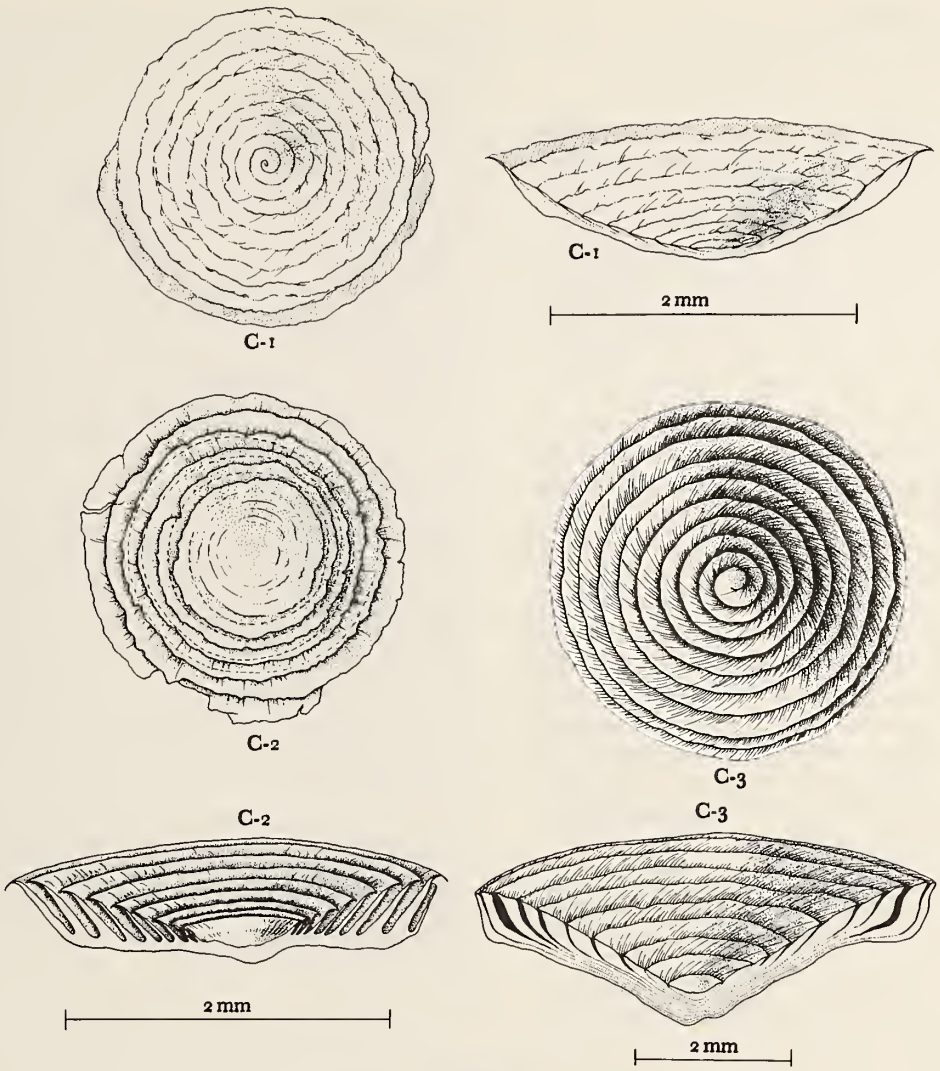


Figure 3

Opercular Types C – 1, C – 2, and C – 3

center. Strongest features of upper surface are many irregularly placed, raised, radial cords. They show up quite well under ordinary light, and are of extreme brightness with transmitted polarized light. Cords occasionally emphasized by parallel (*i.e.*, radial) inclusions of opaque, white, non-calcareous material, possibly mucus. Underside irregular in contour and without elements of true radial or spiral relief. Only very faint traces of horizontal layering seen in cross-section. Specimen illustrated, 3.7 mm in diameter.

Type C-1: polygyrous, thin (Figure 3)

Thin and flexible, of fairly uniform thickness throughout, except for "cellophane edge." No central papilla on undersurface. Flat or concave, depending on contracture of specimen. Upper surface shows many narrow, tightly organized, clearly defined spirals, lying flat and slightly overlapping. Many of these opercula, especially those found in *Ostodes plicatus* and *O. upolensis,* show a silvery, iridescent sheen on the upper surface, which obscures the spirals under ordinary light. With transmitted polarized

light, the sheen disappears and the spirals are revealed. Specimen illustrated, 2.3 mm in diameter.

Type C-2: polygyrous, thick, flat (Figure 3)

Basically flat, with slightly concave central portion; nearly all examples about 4 times as thick near outer margin as through center. Many spiral lamellae, elevated at about 45° angle, surrounding smooth, depressed, central portion. Lamellae thick at base, with outer edges very thin and flexible, curving over inter-lamellar air-space, to touch next outermost lamella and producing a smooth outer surface like that of type C-1. Specimen illustrated, 2.7 mm in diameter.

Type C-3: polygyrous, thick, concave (Figure 3)

Of more uniform thickness from center to edge than type C-2, showing horizontal layering in base more clearly. Most have pronounced central papilla; all very deeply concave. Upper surface resembles type C-1 in having many narrow, clearly defined, tightly organized spirals. Inner structure closer to type C-2 in that spiral lamellae stand up from their bases. Lamellae differ from those of type C-2 in 3 ways: they are generally stouter and heavier; they are differently shaped, being thicker at the upper surface than at the base, and having no thin, overhanging edge; and the spaces between lamellae are not air-spaces, but are filled with an opaque white material, which is not calcareous; it may be mucus. Specimen illustrated 6 mm in diameter.

Discussion: The 6 opercular types are not sex-linked, and are not species-specific. Table 2 lists the distribution of opercular types by species. Three species, *Ostodes llanero, O. reticulatus,* and *O. upolensis,* are known to have only one type of operculum. However, in each case, the opercular type concerned is also found in at least 3 other species. Larger samples of these 3 species probably would include additional opercular types. One type of operculum, type C-3, has been found only in *O. tiara,* which also shows type A-2. I would expect to find additional examples of type C-3 in *O. garretti,* if more individuals of that species were available for examination. Type C-3 is a large, heavy operculum, which would accord as well with the large, heavy shell of *O. garretti,* as do the already-found types A-2 and C-2. From available evidence, I conclude that in *Ostodes* opercular type is not, as has been previously indicated, a diagnostic character at the species level.

The only correlation found between opercular type and habitat is in the 6 specimens of *Ostodes savaii* which had type C-2 opercula. These 6 snails came from a collection station (Station 32, Savaii) having a more pronounced dry season than the other stations on the same island. No species other than *O. savaii* were found there. Of 7 specimens examined for opercula from this lot, 6 had type C-2; the 7th, as well as all other specimens of *O. savaii,* from more uniformly humid places, had thinner opercula (types A-1, B and C-1). A thick operculum would of course convey a selective advantage in a dry season, offering rather more protection against desiccation.

Even this correlation breaks down, however, on Upolu. Of 21 collection stations on that island, there is a cluster of 5 (Stations 5, 7, 14, 16, and 17) that has the same climate

Table 2

Distribution of Opercular Types by Species

Species	A-1	A-2	B	C-1	C-2	C-3	Totals
Ostodes							
adjunctus			1	14			15
exasperatus	7	2	4	3	7		23
garretti	1	2			1		4
gassiesi	19		9	7			35
llanero					3		3
plicatus	8			11			19
reticulatus	8						8
savaii	14		3	7	6		30
strigatus	7	3	15	16	2		43
tiara		3				5	8
upolensis				10			10
Totals	64	10	32	68	19	5	198

as Station 32 on Savaii. Of 17 snails examined for opercula from these 5 stations, 15 were found to have thin opercula. One individual from Station 14 had a thick operculum that appeared to be of type C-1, but with many added layers. There were no upstanding lamellae, as in types C-2 and C-3, there was no central papilla, as in type A-2, and the layers themselves were no thicker than usual for type C-1; there were simply more of them. One individual from Station 17 had a similarly thickened operculum, resembling type A-1, but with many more layers than normal. The "dry stations" on Upolu are in somewhat denser forest than the one "dry station" on Savaii; perhaps there is enough difference in micro-habitat to decrease the selection pressure for thick types of operculum.

As to the very peculiar opercula designated type B, I think it is unlikely that they are replacements for opercula accidentally torn off: Fretter & Graham (1962: 82) describe a replacement operculum as being thickest in the middle and tapering towards the edges, and without "differentiation of structure apart from being laminated," which description does not fit type B at all. It is possible that type B opercula are the product of some disease process or injury to the snail, although no gross abnormalities of shell or body were observed in the snails from which they were taken. Of 43 animals of *Ostodes strigatus* examined for opercula, 15 had type B opercula, and of these, 8 were so deeply concave as to be cone-shaped, with the greatest diameter of the operculum much less than the diameter of the aperture. The snails with these peculiar opercula looked perfectly normal, except that the back of the foot, beneath the operculum, was deeply hollowed out to accept the pointed end of the cone. One such snail, a female, was very carefully dissected, in search of any anatomical abnormality; none was found, except for the hollow place in the foot. Two of the cone-shaped opercula were greatly thickened by a multiplication of layers. Two other very thick opercula were found in *O. strigatus;* one was type B (ordinary flat form), and the other was type A-1.

The 6 opercular types described above have been observed. The reasons for their existence remain to be explained. It would seem that protection against desiccation or predation could be achieved as effectively by a simple multiplication of layers as by the more elaborate methods of thickening each layer as in type A-2 or creating upstanding lamellae, as in types C-2 and C-3. I have no explanation of these differences.

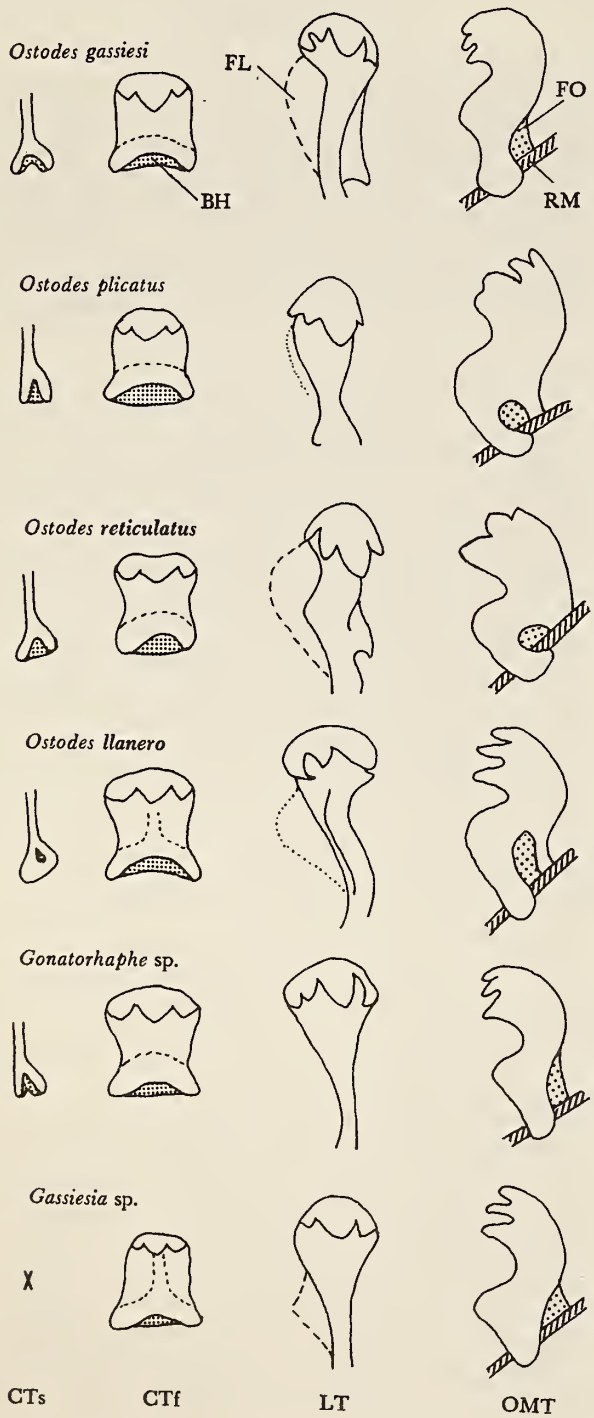
3. RADULAE

(Figures *37–48*)

Cyclophorid snails have a taenioglossate radula, with one lateral tooth and two marginal teeth on either side of the central tooth. Photographs taken with a scanning electron microscope (SEM) show slight differences between genera and species which have not heretofore been noticed. For this study, SEM photographs were taken of the radulae from *Ostodes gassiesi, O. plicatus, O. reticulatus,* and *O. llanero,* plus examples of *Gonatorhaphe* sp. and *Gassiesia* sp. for comparison. The results are summarized below.

Central (rachidian) tooth: In all species examined, the central tooth is tricuspid. The base of the tooth is greatly thickened and deeply hollowed-out from below, with a smaller hollow on each side. When the radula is in the folded position, the central teeth lie in their longitudinal row without touching each other, the curved top of one resting in the space made available by the hollowing of the base of the next anterior tooth (Figure *41*). The shape of the central tooth varies slightly among the species studied. In *Ostodes gassiesi* it is peg-like, appearing of equal width at the level of the cusps, in the middle of the shank, and at the base. The other 3 species of *Ostodes* show central teeth that are slightly flared at the base, and *O. reticulatus* and *O. llanero* also show a slight narrowing above the flare. In *Gonatorhaphe* there is a pronounced narrowing above a moderately flared base. *Gassiesia* shows no narrowing, but a very strong flare is present.

Lateral tooth: The lateral teeth are about twice the length of the central teeth. When the teeth are not in use, the top of each lateral tooth rests against the shank of the tooth next anterior to it, at about the mid-point of the shank (Figures *37, 41*). In the 4 species of *Ostodes* that were examined, the lateral tooth has 4 cusps, of which the most medial is the smallest and the third from the inside is by far the largest. All *Ostodes* lateral teeth have long, slender shanks. In *O. gassiesi* and *O. reticulatus,* there is a medially projecting flange that seems to join the tooth to the radular membrane. The flange is less clearly seen in the photographs of *O. plicatus* and *O. llanero,* but it is shown in Thiele's drawing of the radula of *Maizania preussi* (Thiele, 1929: 99; fig. 76). In *Gonatorhaphe* sp. the lateral tooth still has 4 cusps, but the medial one is much reduced. The shank is long and slender, and there is no flange. In *Gassiesia* sp. the long shank has a flange,



but the tooth has only 3 cusps – the most medial cusp has disappeared altogether.

Marginal teeth: The viewing angles are such that the inner marginal tooth cannot be seen consistently and clearly enough for comparative discussion. The outer marginal tooth is seen clearly, however, and shows more variation than any of the other radular teeth. The tooth always has 3 (some views of *Ostodes gassiesi* seem to show 4) cusps. The cusps are pointed, except in *O. plicatus,* where the outermost one is truncated. Below the outermost cusp, the outline of the tooth is first deeply indented and then protrudes into a sharply angled "shoulder." In the folded position, the outer edge of the inner marginal tooth is cradled in the indentation of the outer marginal tooth (see Figures *38* and *46*). Below the "shoulder" a shank of moderate length connects the tooth to the radular membrane. In the lower extremity of the shank there is a foramen through which the radular membrane passes. This arrangement permits the tooth to grasp the edge of the membrane firmly, but with the potential for a great deal of movement, due to the size and shape of the foramen. The angles of the indentation and "shoulder," as well as the character of the foramen, vary from species to species, and are summarized in Table 3. The functional significance of the differences in the foramen is unknown.

Discussion: Figure 4 shows 3 teeth from one row of the radula of each of the 6 species studied, presented together for ease of comparison. The differences between the 4 species of *Ostodes* are so slight that I do not feel they could be used as a diagnostic character. The teeth of *Gonotorhaphe* seem to be a sort of mixture: the central tooth resembles that of *O. **reticulatus,*** the lateral tooth resembles the lateral tooth of *O. **llanero,*** and the outer marginal tooth is very similar to the corresponding tooth of *O. gassiesi*. I would hesitate to try to differentiate between *Gonotorhaphe* and *Ostodes* on the basis of their teeth. The teeth of *Gassiesia,* however, are very different from those of the other 2 genera. The strongly flaring central tooth; the lateral tooth with only 3, not 4, cusps; and the very broad, low foramen in the outer marginal tooth set this

(← adjacent column)

Figure 4

Comparison of Radular Teeth of Six Poteriid Species

BH – basal hollow CTf – frontal view of central tooth
CTs – side view of central tooth FL – flange FO – foramen
LT – lateral tooth OMT – outer marginal tooth
RM – radular membrane

Table 3

Character of Outer Marginal Tooth

Species	Angle of indentation	Angle of shoulder	Character of foramen
Ostodes gassiesi	30°—45°	60°—90°	broad, squarish
Ostodes plicatus	75°	90°	broad, low
Ostodes reticulatus	60°	90°	broad, low
Ostodes llanero	45°	90°	tall and narrow
Gonatorhaphe sp.	45°	90°	very tall, pointed top
Gassiesia sp.	60°	90°	very broad, low

radula apart from the others quite clearly. These radular differences are sufficiently clear-cut to be a useful diagnostic character.

4. GROSS ANATOMY

a. General: Uppermost part of visceral hump occupied entirely by testis in male; in female, ovary lies on columellar side, digestive gland on outer side. Middle portion of visceral hump occupied entirely by digestive system in both sexes, except for passage of gonoduct on columellar aspect. Lowest part of visceral mass in both sexes has reproductive organs on columellar side, digestive system on outer side.

Position of organs in pallial cavity as follows: on right side, gonoduct runs below rectum from mantle line nearly to anterior opening of cavity. On left, kidney lies between layers of mantle, extending forward to about middle of pallial cavity. Pallial renal orifice not located. Pericardial cavity, with heart, nestles against lower middle portion of kidney. Hypobranchial gland J-shaped, beginning to left of mid-line, passing transversely behind kidney, then turning to run anteriorly between upper renal margin and rectum. Point of origin of transverse portion, and length and thickness of anterior portion of hypobranchial gland differ in the several species, and will be discussed individually. Anterior portion of mantle thin, fragile, vascular, except for thickened leading edge.

b. Digestive system: In female, digestive gland reaches apex of visceral mass, surrounding ovary for approximately first whorl, except on columellar side. In male, digestive gland begins at lower edge of testis. Stomach embedded in outer side of digestive gland and visible through integument. In both sexes, stomach and digestive gland together occupy entire lumen of whorl, in middle section of visceral hump, except for passage of gonoduct and esophagus on columellar side. Massed loops of intestine occupy outer half of anterior visceral hump, with most distal segment crossing from left to right just behind mantle cavity. Intestine continues forward as rectum between layers of mantle on right side. Anal orifice just inside leading edge of mantle. In males, anal orifice points straight forward. In females, orientation of anal orifice and degree of hypertrophy of its edges are species-specific.

c. Male reproductive system (Figure 5): Testis fills entire lumen of first 1—2 whorls, depending on age of individual. Color ranges from uniform creamy white through tan and brown to very dark grey. Younger individuals have smaller and lighter-colored testes. Color caused by pigment granules which appear on surfaces of testicular tissue lobules, and in interlobular spaces. In young adults they are light brown, small in size, and scattered sparsely but fairly evenly, giving whole organ a tan color, rather than the cream of the juvenile. As snail ages, granules increase in size, number, and intensity of color, causing whole organ to appear darker and darker. In an occasional individual, the granules will cluster into scattered black blotches; sometimes granules are also found on the inner surface of the encapsulating membrane. The pigment granules, whether clustered or single, are not usually firmly adherent to testicular tissue, but may be picked off fairly easily, revealing tissue itself, still creamy white underneath.

Testicular tissue consists of a number of multiple-branched trees of digitiform alveoli, arranged in a single row on the outer side of a single collecting tube, which runs down the columellar side of the whorl. Each major alveolar trunk or duct divides into 2 equal main branches, which in turn divide and re-divide fairly symmetrically. Outermost tips of the terminal alveoli give surface of the organ a lobulated appearance. There are at least 3 major alveolar ducts near anterior end of testis, with an undetermined number of progressively smaller ducts running back toward the posterior tip of the organ. Even in deeply pigmented testes, the collecting tube, and in some cases, the major ducts, are without pigment granules and thus appear white.

Collecting tube runs forward as seminal vesicle on columellar side of visceral mass. In central visceral section, it lies lateral to the esophagus and ventral to the stomach.

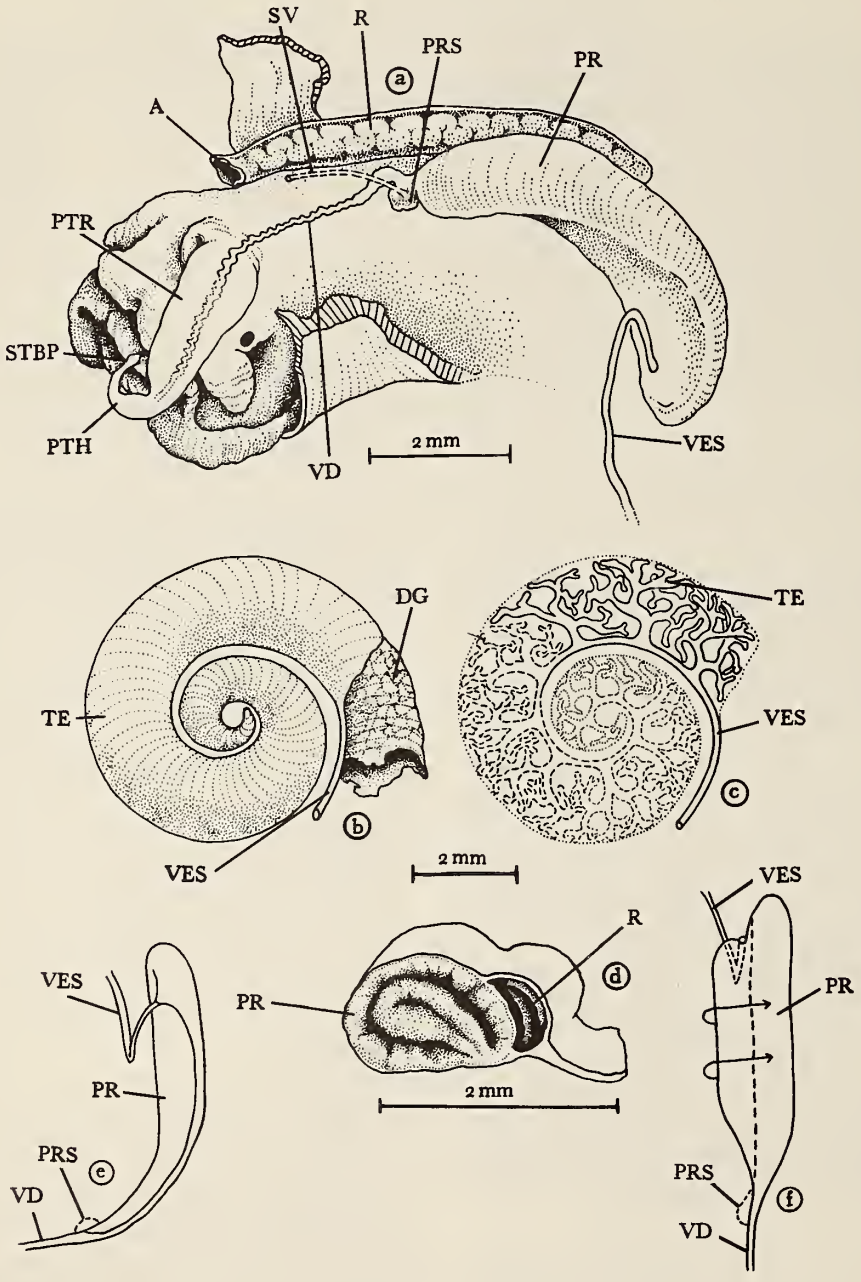


Figure 5

Elements of the male reproductive system in *Ostodes*

a – generalized composite male, view from above b – testis external appearance; c – testis, internal arrangement, diagrammatic; d – cross-section of prostate; e – diagram showing folded structure of prostate, seen from underside; f – diagram showing prostate unfolded, seen from underside [for explanation of abbreviations see Appendix on foldout]

After passing proximal tip of prostate, it turns sharply upon itself and runs back to enter ventral surface of prostate slightly anterior to its proximal end.

Prostate creamy white, visible through integument on columellar side of body. Structure of prostate resembles a sandwich, sealed around the edges, and folded in half longitudinally, slightly off center. This structure gives a cross-section with 2 layers of bread (prostatic tissue) in the middle, the sandwich filling (lumen of the prostate) lying in a U-shape, and another layer of bread (prostatic tissue) around the outside of the U (see Figures 5d, 5e, 5f). Most proximal portion of prostate, which lies beneath distal end of digestive gland, is flattened dorso-ventrally, more anterior portions oval to round. Medial upper aspect of prostate touching intestinal loops.

Prostate enters pallial cavity on right side, within mantle wall, below rectum and in angle formed by juncture of mantle and body. Prostate terminates in a blunt tip at about mid-point of pallial cavity. In some specimens, the prostatic tip is truncated. In others, there is a constriction of the medial half of the organ, a short distance behind the tip, resulting in the presence of a small pouch or sac on the anterior medial corner of the prostate. The presence of this sac is in part a function of age, in part of species. Juveniles almost never have sacs; adults are more likely to have sacs in some species than in others. Table 4 shows the frequency of occurrence of sacs, and also of a small, fragile duct, of varying origin and termination, which appears to be a "safety-valve" for venting excess sperm (see FRETTER & GRAHAM, 1962: 345, 348). There is no correlation between presence or absence of a sac and presence or absence of a "safety-valve." If a "safety-valve" occurs in a specimen having a sac, the most usual origin of the duct is the dorsum of the sac. In a snail without a sac, the most usual origin of the duct is the medial anterior corner of the truncated prostate. In either case, the duct usually runs laterally and anteriorly across the base of the vas deferens, and terminates beneath and slightly behind the anal orifice. Variations from these patterns are mentioned in the species descriptions.

Table 4

Prostatic Characters (mixed ages)

Species	Presence of Sac	Presence of "Safety-Valve"
Ostodes		
adjunctus	0 of 4	0 of 4
exasperatus	2 of 5	1 of 5
garretti	2 of 2	1 of 2
gassiesi	11 of 15	2 of 14
llanero	0 of 1	0 of 1
plicatus	1 of 5	4 of 5
reticulatus	3 of 3	3 of 3
savaii	10 of 13	5 of 14
strigatus	0 of 6	0 of 6
tiara ("smooth")	1 of 5	4 of 5
tiara ("bumpy")	1 of 1	1 of 1
upolensis	3 of 4	4 of 4

Vas deferens originates from anterior lateral corner of prostate. It is a closed tube running anteriorly and medially beneath the skin to the base of the penis, where it passes upwards, lying at first near the surface, but penetrating progressively more deeply, to reach the center of the penis about half-way up the trunk. TIELECKE (1940: 332) states that males of *Ostodes strigatus* have an open sperm groove. I have not seen the specimens on which he based his statement, and so do not know what species he actually had before him. The 64 males of *O. strigatus* available to me agree with Gould's original description and figure for *O. strigatus* (GOULD, 1848: 204–205; 1852: 102–103; 1860: plt. 8, figs. 117, 117a, 117b), and they all have closed vasa deferentia.

Penis on cephalic mid-line, just posterior to tentacles. Base usually thick, somewhat rugose, probably partly contractile but not introversible. The ovoid to rounded trunk narrows gradually to abruptly into a thin distal thread, which may be long or short in proportion to the trunk. Some specimens have a sub-terminal bulb or swelling on the thread; there is no correlation between presence or absence of a bulb and length of thread. Penis usually carried folded sharply back from its base, the whole length of the trunk lying flat along the neck and body inside the mantle cavity. There is another sharp fold at the base of the distal thread, which lies folded against the trunk, the tip pointing forward. In the case of a very long thread, or a thread with a sub-terminal bulb, the tip sometimes may be found folded under. The ratio of thread-length (including taper) to trunk-length is diagnostic at the species level. Ratios for adults of the several species are found in Table 5. For discussion purposes, a specimen is considered to have a short thread if the ratio of thread to trunk is 1/1.6 or more. This ratio was chosen as the dividing point because, on a graph showing the thread to trunk ratio of every available specimen of *Ostodes gassiesi* (a consistently short-threaded species) and *O. plicatus* (a consistently long-threaded species), 95% of *O. gassiesi* specimens had ratios of 1/1.7 or more, while 97% of *O. plicatus* specimens had ratios of 1/1.5 or less. Although the lengths of thread and trunk differ from species to species, the total length of the penis is fairly uniform, at least among the mid-sized species (Figure 6).

Table 5

Penial Characters

Species	Bulb present on thread (mixed ages)	Ratio of thread length to trunk length (adult)					
		Short thread			Long thread		
		N	Range	Mean	N	Range	Mean
Ostodes							
adjunctus	0 of 11	2	1/1.7-1/1.5	1/2.1	9	1/0.5-1/1.5	1/0.97
exasperatus							
(Upolu)	1 of 4	0	–	–	4	1/1.05-1/1.5	1/1.22
(Savaii)	4 of 6	4	1/2.5-1/7.3	1/4.68	2	both 1/1.5	1/1.5
garretti	0 of 2	0	–	–	2	1/1.4-1/1.6	1/1.5
gassiesi							
(all)	7 of 12	53	1/1.7-1/11	1/4.73	3	1/0.86-1/1.43	1/1.12
(Upolu)	5 of 7	36	1/1.7-1/10	1/3.8	2	1/0.86-1/1.43	1/1.13
(Savaii)	2 of 5	17	1/2.7-1/11	1/6.7	1	–	1/1.1
llanero	0 of 1	0	–	–	1	–	approx. 1/1.2
plicatus	0 of 5	1	–	1/1.7	31	1/0.25-1/1.5	1/0.98
reticulatus	0 of 3	0	–	–	5	1/0.46-1/1.25	1/0.91
savaii							
(all)	11 of 23	43	1/1.7-1/10	1/3.66	7	1/1 -1/1.5	1/1.3
(Upolu)	2 of 5	14	1/2.0-1/4.5	1/3.0	2	1/1.38-1/1.5	1/1.44
(Savaii)	9 of 17	29	1/1.7-1/10	1/3.97	5	1/1 -1/1.5	1/1.24
strigatus	0 of 43	0	–	–	43	1/0.31-1/1.20	1/0.60
tiara							
("smooth")	0 of 6	0	–	–	6	1/0.54-1/1.5	1/0.93
("bumpy")	2 of 2	2	thread/collar/trunk 1/0.22/1.67	1/0.2/1.8	0	–	–
			1/0.22/1.85				
upolensis	0 of 2	1	–	1/2.2	6	1/0.54-1/1.5	1/1.15

In both *Ostodes gassiesi* and *O. savaii,* short-threaded specimens from Savaii have shorter threads than comparable individuals from Upolu. I have been unable to find any reason for this difference. There are no important conchological differences between snails from the two islands, nor are there significant differences between long-thread and short-thread snails of the same species. In *O. **exasperatus,*** all males from Upolu are long-threaded, while the Savaii population has 67% with short threads. The shells from the two populations are not significantly different, and the female reproductive systems are virtually identical.

Explanation of Figures *37* to *42*

Figure *37*: *Ostodes gassiesi*, central tooth and tetracuspid lateral teeth × 477

Figure *38*: *Ostodes gassiesi*, radula in folded position, showing edge of radular membrane and foramina in outer marginal teeth × 509

Figure *39*: *Ostodes plicatus*, central tooth, showing hollowed-out base; tetracuspid lateral teeth and inner marginal teeth × 478

Figure *40*: *Ostodes plicatus*, edge of radular membrane and outer marginal teeth with foramina × 360

Figure *41*: *Ostodes **reticulatus***, central teeth, tetracuspid lateral teeth, and inner marginal teeth × 368

Figure *42*: *Ostodes **reticulatus***, outer marginal teeth, showing foramina × 1115


37


38


39


40


41


42

Ostodes tiara presents special problems. Sixteen male specimens, 9 adults and 7 juveniles, from 5 different localities, were examined. One was a freak, having a penis with three threads. Ten, 6 adults and 4 juveniles, had standard long-thread penes. These (Figure 7a) are referred to in the tables as "smooth." Some males with "smooth" penes were found at each of the 5 localities. At Station 8, on Upolu, in addition to 3 males with "smooth" penes, 2 adults and 3 juveniles were found with a very different type of penis, referred to as "bumpy." The trunk is surmounted by a white bump, resembling a knuckle. Beyond the bump is a constricted portion, or collar, which may be slightly reddish, and which is followed by a short swollen area which tapers to a short thread with a sub-terminal bulb (Figure 7b). Males with this type of penis have umbilici averaging 15.4% larger than those of "smooth" penis males. The females from Station 8 also had larger umbilici than females from the other stations. No other statistically significant conchological differences were found, nor did the female reproductive systems from Station 8 have any unusual features.

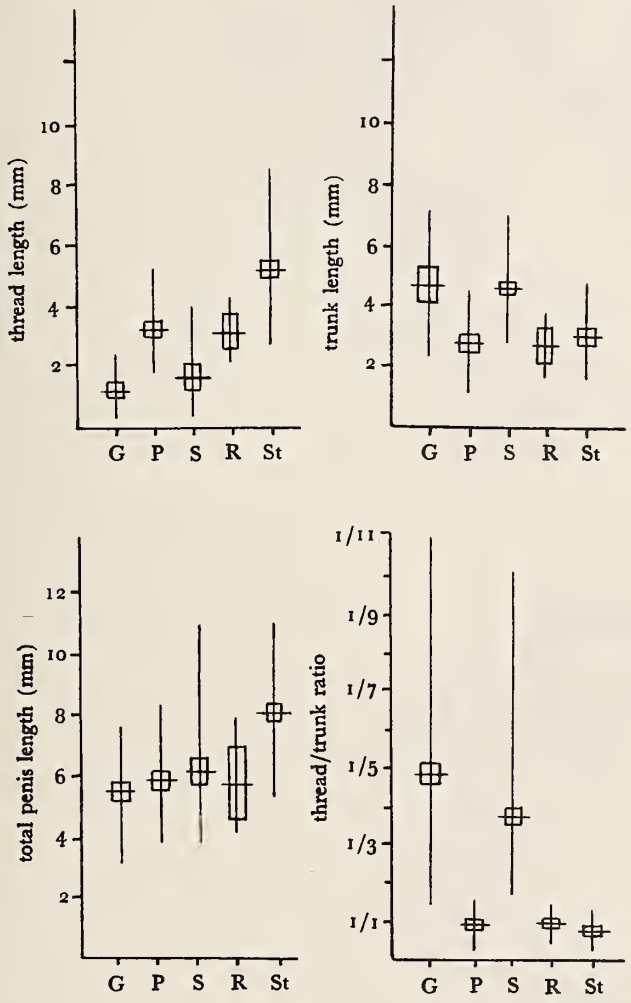


Figure 6

Lengths of penis thread, penis trunk, and whole penis, and ratios of thread length to trunk length, in five mid-sized species of *Ostodes*

G – *Ostodes gassiesi*; P – *O. plicatus*; R – *O. reticulatus* S – *O. savaii*; St – *O. strigatus* — vertical line – range of measurements; horizontal line – mean; hollow box – two standard errors of the mean on either side of the mean

d. Female reproductive system (Figures 8, a, b; 9): Ovary begins slightly anterior to apex of visceral hump and occupies columellar side for approximately one whorl. Ovarian tissue composed of a mass of white granules of irregularly spherical contour, held together by an encapsulating membrane, but not otherwise macroscopically organized. There is no system of collecting tubules equivalent to that of the male testis. The ovary tapers anteriorly to a blunt point, with the encapsulating membrane continuing forward as the oviduct. Oviduct lies on columellar side of body, lateral to esophagus and ventral to stomach and digestive gland, running anteriorly nearly to mantle line, then reflexing sharply upon itself and continuing up to approximately the level of the uterine fundus; reflexes again and runs downward for a short distance.

Slightly below level of uterine fundus, oviduct becomes progressively thicker and begins to fold upon itself accordion-fashion in a single plane. There are from 3 to 6 foldings, each slightly deeper than the preceding one. The folds nearest the columella are laid down even with each other, with the increasing depth of the folds producing a triangular mass, lying ventral to the uterus, its long axis parallel to the long axis of the visceral hump. The folds are held together by an encapsulating membrane which is transparent and covered with brown speckles, which are most numerous in the valleys between folds. I believe that this area of folded oviduct serves as a seminal receptacle (Figure 9a).

Distal to the seminal receptacle, the now quite thick oviduct is joined, on its lateral aspect, by an equally thick duct which leads away from the columella to a large, heavily pigmented, bulbous structure, which I believe to be a bursa copulatrix. It lies partly beneath the uterus but mostly ventral to the mass of intestinal loops. If distended, it can often be seen through the integument of the visceral mass, just behind the kidney at the mantle line. If not distended, it resembles a collapsed balloon, lying beneath the intestine. The pigment particles lie

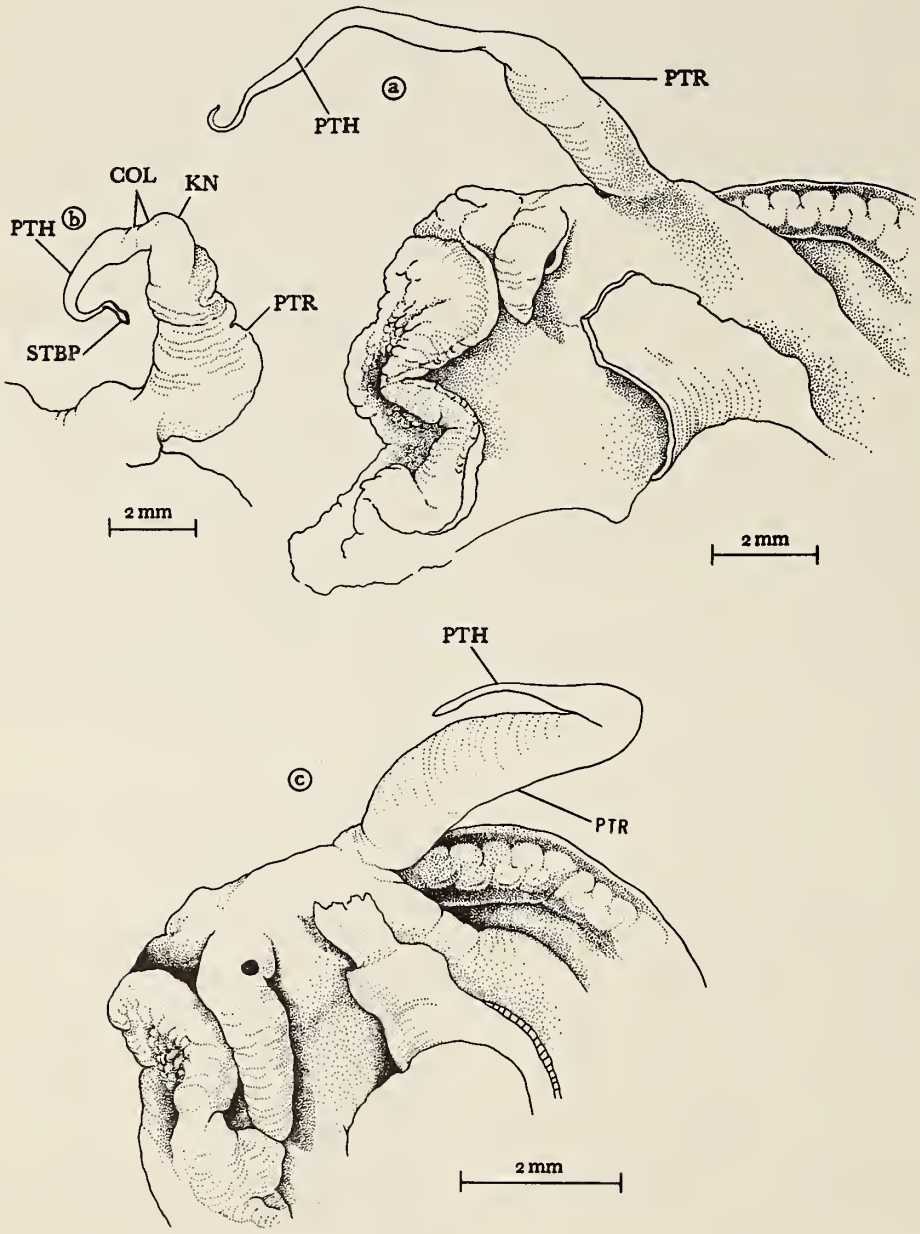


Figure 7

Penis types in *Ostodes tiara* and *Ostodes garretti*
a – *O. tiara*, "smooth"; b – *O. tiara*, "bumpy";
c – *O. garretti*
[for explanation of abbreviations see Appendix on foldout]

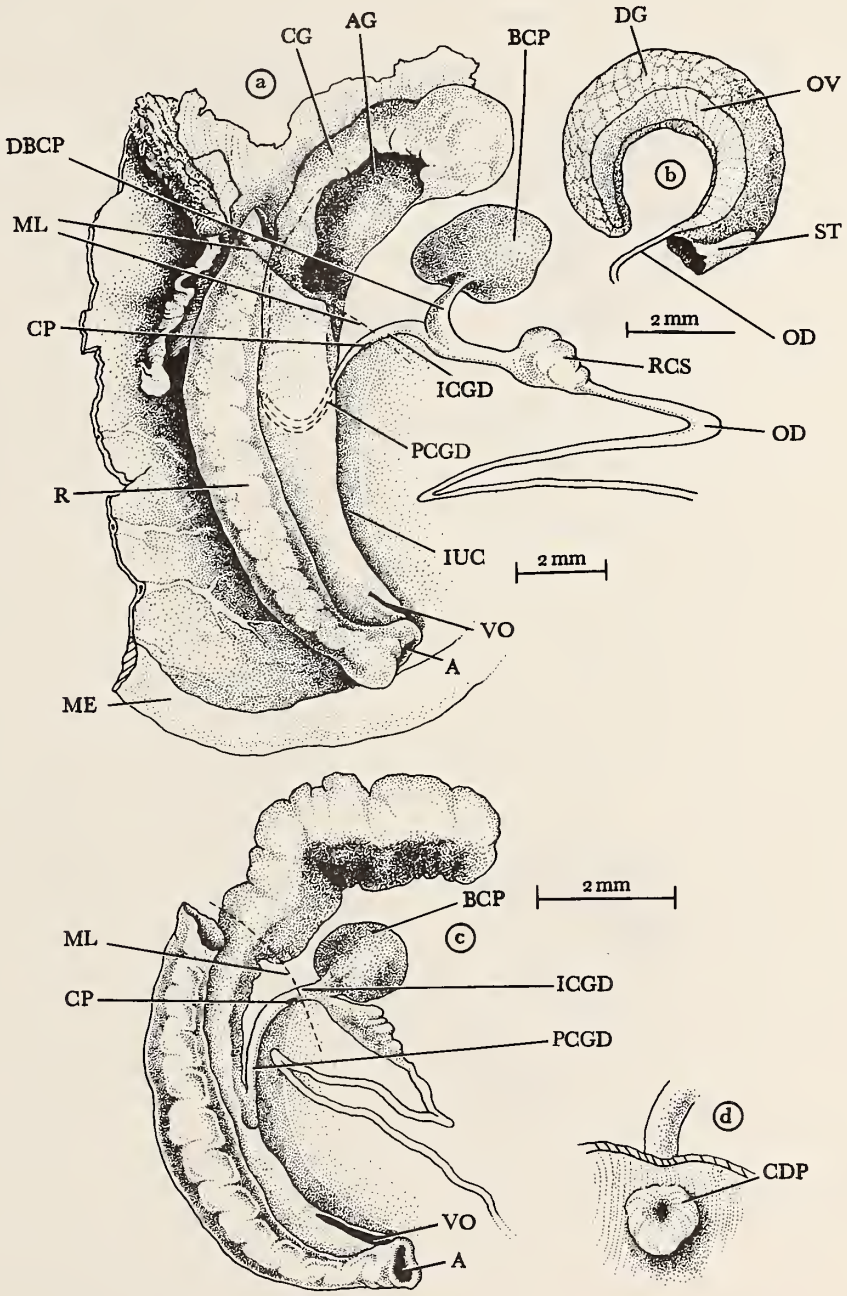


Figure 8

Female reproductive system in *Ostodes tiara* and *Ostodes garretti*

a – *O. tiara*; b – *O. tiara*, ovary; c – *O. garretti;*
d – *O. garretti*, entrance of common genital duct into uterus
[for explanation of abbreviations see Appendix on foldout]

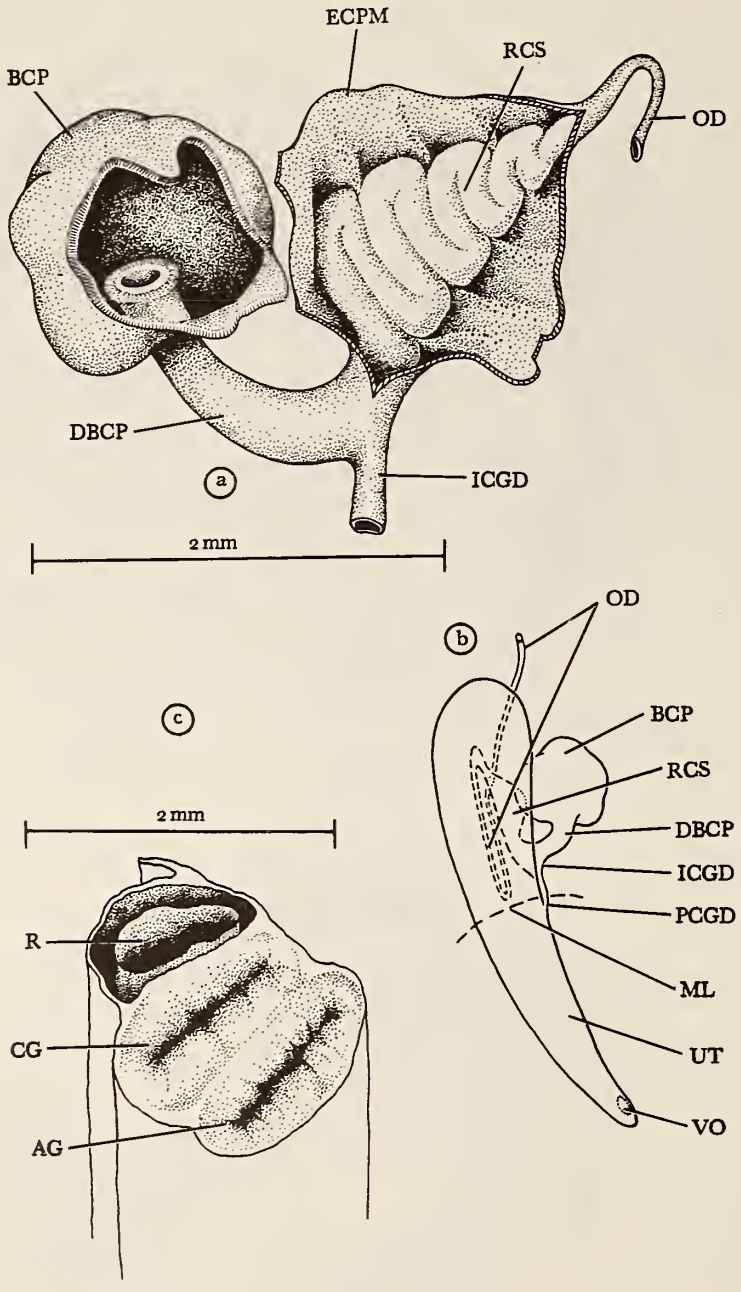


Figure 9

Generalized details of female reproductive system in *Ostodes*

a – cutaway views of bursa copulatrix and seminal receptacle
b – diagram showing elements of reproductive system in true anatomical relationship
c – cross-section of uterus
[for explanation of abbreviations see Appendix on foldout]

partly on the covering membrane, and partly on the outer surface of the wall itself. The walls are thick and soft, and appear to be constructed of fibers laid vertically to the lumen of the organ. The inner surface is soft and creamy white. The duct protrudes part way into the lumen, which is sometimes found filled with a pearly white amorphous mass.

Previous workers do not agree concerning the probable function and nomenclature of the folded oviducal area and pigmented sac. Tielecke (1940: 331–332) called the folded area of *Ostodes strigatus* a seminal receptacle and the pigmented sac a bursa copulatrix. Thompson (1969: 40–41), working on Central American cyclophorids, called the folded area an albumin gland and the pigmented sac a seminal receptacle. Neither gives histological details to support his conclusions.

Work on *Pomatias elegans* (Creek, 1951) and *Acme fusca* (Creek, 1953) did involve histological examination of the entire genital tract, extensive tissue staining studies, and laboratory observations of breeding and egg laying. In *Pomatias elegans* there is a widened muscular section of the renal oviduct which functions as a seminal receptacle, its walls being covered with large numbers of orientated sperm at all seasons of the year (Creek, 1951: 606). There is a sac at the posterior end of the pallial oviduct, which although homologous with the seminal receptacle of many other gastropods, functions as a bursa copulatrix (Creek, *op. cit.*: 636). This bursa opens directly into the mantle cavity, and the penis is actually inserted into this sac at copulation (Creek, *op. cit.*: 606). In *Acme fusca,* however, the bursa opens to the mantle cavity by means of a duct, and the penis probably does not actually enter it during copulation (Creek, 1953: 234). As in *Pomatias,* the anterior portion of the renal oviduct is convoluted and slightly swollen. This area, homologous to the seminal receptacle of *Pomatias,* probably functions in *Acme* as a fertilization chamber, as it has been found to contain ingesting cells for the disposal of excess sperm.

The structures in *Ostodes* are very similar to those found in *Acme.* Both genera show a thickening of the anterior renal oviduct; both have a sac-like structure located near the upper end of the uterus; both have a duct leading from the mantle cavity to the sac, the renal oviduct, and the uterus. I do not know exactly where fertilization takes place, but the pigmented sac in *Ostodes* certainly seems to function as a bursa copulatrix, and I therefore agree with Tielecke and call the thickened area of the renal oviduct the seminal receptacle.

Distal to the entrance of the duct from the bursa copulatrix, the oviduct, now a common genital duct, again becomes thin and fragile. The length of the common duct, from the junction of the ducts from bursa and receptacle to the mantle line, varies greatly from species to species (see descriptions). The common duct enters the pallial cavity and continues downward along the medial margin of the uterus, to which it is bound by a thin sheet of tissue. There is a small hole, the copulatory pore, in the medial aspect of the genital duct. This is located between the posterior margin of the mantle cavity and the point of entry of the genital duct into the uterus, its position varying with the species. The copulatory pore is the posterior termination of a channel which is formed by an overlayment of the uterus onto the right side of the mantle cavity floor. The medial margin of the channel is formed by a very slight ridge in the body tissues, and when the mantle is in its normal position (not laid back as for dissection) the channel would function as a closed tube. There is no grossly visible specialization of the tissues forming the channel floor. Whether this channel serves to guide the penis to the copulatory pore, or as a passageway for sperm deposited at its anterior end, must remain a matter for speculation until behavioral studies can be made.

Uterus lies along columellar side of body, partly within visceral hump beneath most anterior portion of digestive gland, and partly at right side of pallial cavity, below rectum. Uterus bi-lobed, ventral lobe occupying the middle half to three-fourths of dorsal lobe length. Dorsal lobe overlies upper end of ventral lobe, folding upon itself to form entire uterine fundus, and continuing forward, past anterior end of ventral lobe, to form entire vaginal portion of uterus. In cross-section (Figure 9c) it is seen that the two lobes are entirely separate, except for a proximal end-to-end anastomosis, so that the lumen of the uterus is one continuous passage from the anterior end of the ventral lobe, up around the fundus, and down the length of the dorsal lobe to the vaginal orifice. The texture of the two lobes is quite different. The ventral lobe is composed of firm, densely packed, fine-grained tissue which is often pink in color, especially near the anterior end. The tissues of the dorsal lobe are creamy white, and appear softer, more friable, and more loosely organized. Dorsal lobe passes forward, beneath the rectum, toward the front of the pallial cavity. Vaginal orifice near anus. The shapes, sizes, and orientations of these 2 openings are species-specific, and will be discussed in the species descriptions.

5. SEXUAL DIMORPHISM

For this study, there were available 13 populations of *Ostodes* which contained both adult males and adult females. Ten of the 12 species were included in the 13 populations: *O. plicatus, O. reticulatus, O. upolensis, O.*

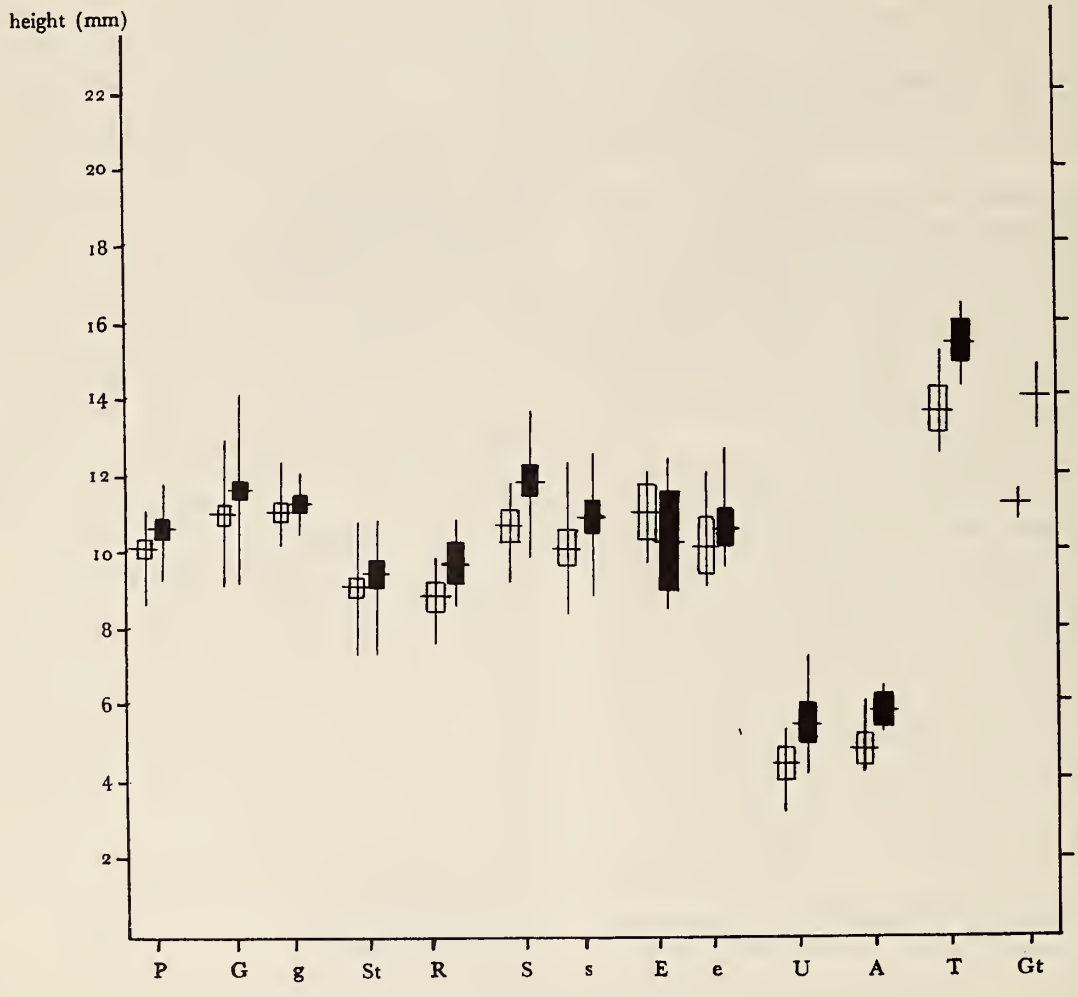


Figure 10a

Sexual dimorphism in height in ten species of *Ostodes* (adults) A – *Ostodes adjunctus*; E – *O. exasperatus*, Upolu population; e – *O. exasperatus*, Savaii population; G – *O. gassiesi*, Upolu population; g – *O. gassiesi*, Savaii population; Gt – *O. garretti*; P – *O. plicatus*; R – *O. reticulatus*; S – *O. savaii*, Upolu population; s – *O. savaii*, Savaii population; St – *O. strigatus*; T – *O. tiara*; U – *O. upolensis*. Vertical line – range of measurements; horizontal line – mean; box – two standard errors of mean on either side of mean; hollow box – male; solid box – female

tiara, O. garretti, O. adjunctus, and *O. strigatus* were represented by one population each, while *O. gassiesi, O. savaii,* and *O. exasperatus* were represented by one population from Upolu and another from Savaii. Only juvenile shells of *O. llanero* were available, and only one empty shell of *O. cookei* was seen.

When the shell measurements of males and females of the above-named 13 populations are examined, the usual pattern is seen to be that females are both taller and wider than males of approximately the same whorl-count (Figures 10a, b). The only population in which this situation is reversed is that of *Ostodes exasperatus* on Upolu; at a very

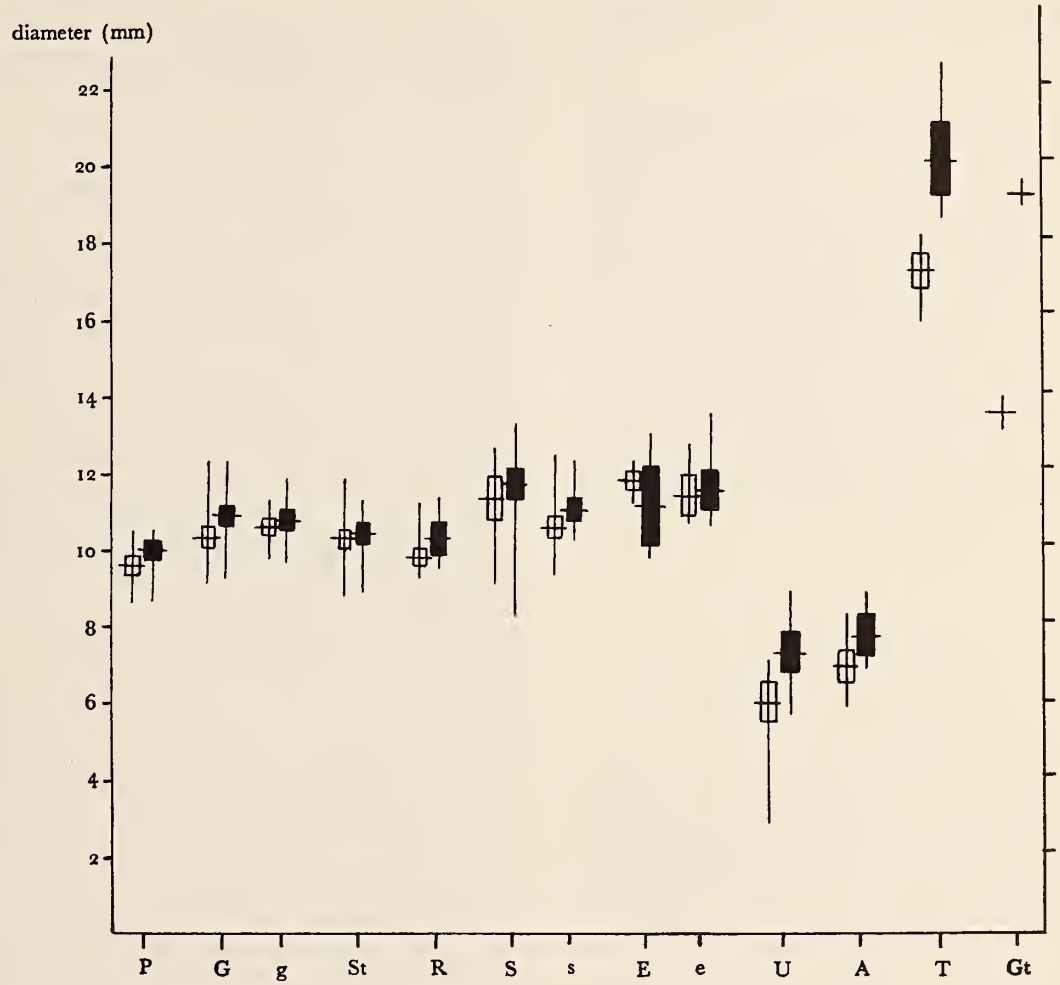


Figure 10b

Sexual dimorphism in diameter in ten species of *Ostodes* (adults)
[for explanation of symbols see Figure 10a]

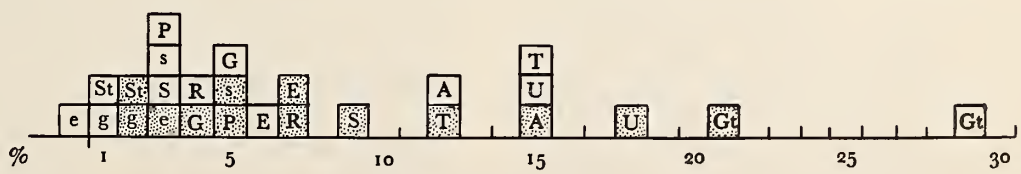


Figure 11

Percentage differences in mean height and diameter between males and females in 13 populations of *Ostodes*. Species designations as in Figure 10a

difference in diameter

difference in height

slightly lower whorl-count, males average 0.75 mm higher and 0.69 mm wider than females. The Savaii population of *O. **exasperatus*** follows the usual pattern of larger females.

Male-female differences in height are slightly greater than differences in diameter in 10 of the 13 populations. The differences are usually rather small, nearly three-fourths of them being 9% or less, with the remainder widely scattered between 12% and 29%. Figure 11 shows the distribution of percentage differences. It is interesting that the greatest differences occur in the smallest and largest species; in little *Ostodes upolensis,* females average 18% taller and 15% wider than males; in *O. adjunctus,* the differences are 15% and 12%, respectively. In the largest species, *O. tiara,* females are 12% taller and 15% wider. The greatest differences of all occur in the second-largest species, *O. garretti,* its females are 21% taller and 29% wider than males at very nearly the same whorl count ($\bar{X}W = 5.22$ female, 5.19 male).

B. Systematic Accounts

1. The GENUS *Ostodes* Gould, 1862

Gould, 1862, Proc. Boston Soc. Nat. Hist., 8: 283; Kobelt & von Möllendorff, 1897, Deutsche Malak. Ges., Nachr., 29: 112; Kobelt, 1902, Das Tierreich, 16: 153, fig. 32 (*O. plicatus*); Thiele, 1929, Handb. syst. Weicht., 1: 99; Tielecke, 1940, Arch. f. Naturgesch., N. F., 9: 331, 332. 350, 361, 362, 364, figs. 7, 8, 19 (*O. strigatus* [?], male and female genitalia and nervous system); Clench, 1949, Bull. B. P. Bishop Mus., 196: 9–10.

Type species: *Cyclostoma strigatum* Gould, 1848, by OD.

Shell narrowly to broadly turbinate, spire elevated. Thin and fragile to thick, heavy, and strong. Small (3.2 mm high X 2.8 mm wide) to large (12.5 mm X 22.5 mm). Females average larger than males at same whorl-count, except Upolu population of *Ostodes **exasperatus***. Four to 6 whorls, spire angle 70° – 120°. Aperture round, holostomatous, appressed to whorl above; outer lip simple, parietal callus thin to thick. Umbilicus deep, narrow to wide; may be smoothly rounded, sharply angled, or bordered by rim. Apical whorls smooth. Later whorls show spiral lirae, radial plicae, or both, except *O. cookei,* which is smooth. Terminal portion of body whorl of adults indented under penultimate whorl, except *O. adjunctus*. Periostracum thin, yellowish to dark brown, adherent or deciduous. Color cream to dirty white, sometimes with pink to red spire. Operculum round, corneous, transparent, thin to thick, with many or few volutions, or laminate.

Penis external, on dorsal midline of head behind tentacles, with closed vas deferens and terminal thread. Oviduct, seminal receptacle, and bursa copulatrix discharge into uterus via common genital duct, wherein is copulatory pore.

2. KEY to the SPECIES

1 a Adult shell smaller than 7.5 mm high by 8 mm wide 2
b Adult shell larger than above 4
2 a Shell smooth ..... *O. cookei*
b Shell with distinct sculpture 3
3 a Strong spiral sculpture on ventral surface, umbilicus with bordering rim; from Tutuila ..... *O. adjunctus*
b Ventral spirals weak or absent, umbilicus without a rim; from Upolu or Savaii ..... *O. upolensis*
4 a Shell as high as or higher than wide 5
b Shell wider than high 7
5 a Shell with very prominent radial plicae 6
b Radial plicae weak or absent, spiral lirae strong ..... *O. savaii*
6 a Radial plicae very prominent, spiral lirae evenly distributed on whorls, ventral surface with radial plicae; females with rectum and vagina bent downward, males with long-threaded penes ..... *O. plicatus*
b Radial plicae broad and low, spiral lirae concentrated on lower half of whorl, ventral surface smooth; females with straight anus and vagina, males with short-threaded penes *O. gassiesi*
7 a Radial plicae and spiral lirae of approximately equal prominence, making a reticulated surface ..... *O. **reticulatus***
b Spiral lirae predominant 8
8 a Spire angle less than 100° 9
b Spire angle more than 100° 10
9 a Ventral surface smooth; from Tutuila ..*O. strigatus*
b Ventral surface with spiral sculpture; from Upolu or Savaii ..... *O. **exasperatus***
10 a Shell smaller than 10.5 mm high by 13 mm wide ..... *O. **llanero***
b Shell larger than above 11
11 a Posterior part of hypobranchial gland thick and heavy; from Upolu ..... *O. tiara*
b Posterior part of hypobranchial gland much reduced; from Savaii ..... *O. garretti*

3. CRITERIA FOR SPECIES RECOGNITION

In order for 2 taxa to be recognized as separate species, they must display significant differences, not only in the shell, but also in the anatomy. The greater the number of differences in unrelated systems, and the greater the magnitude of the differences, the greater the probability that the 2 taxa really are different. To illustrate, let us consider 3 specific cases: one in which a few important differences made the species decision easy; one in which a number of smaller differences made the separation harder; and one in which the differences were deemed insufficient to warrant separation of taxa.

The first case is that of *Ostodes plicatus* vs. *O. gassiesi*. Both taxa have shells of approximately the same size and shape – higher than wide, and with narrow umbilici. Neither has any sculptural element that is totally lacking in the other; the conchological differences lie in the distribution of the spiral lirae, and the distribution and relative prominence of the radial plicae. The shell differences, though present and consistent, would not be sufficient ground for separating the 2 taxa, were it not for anatomical differences of much greater magnitude. In *O. plicatus*, the males almost always have penes with long, bulbless threads, and the females almost always have a distinctive downward bend in the terminal portions of rectum and vagina. In *O. gassiesi*, the female openings point directly forward, and the males have short-threaded penes, often with sub-terminal bulbs. The relatively minor differences in sculpture, plus the major differences in genitalia, give ample evidence for the designation of these 2 taxa as separate species.

The second case, that of *Ostodes savaii* vs. *O. **exasperatus*** is less clear-cut. Individuals of *O. **exasperatus*** differ conchologically from those of *O. savaii* in height, width, umbilical diameter, and contour – all elements which are influenced by the single factor of rate of decoiling – and in having more whorls for their size than does *O. savaii* (Figure 12). They also differ in sculpture, in that radial plicae are totally lacking in *O. **exasperatus***, while they are present, though unobtrusive, in *O. savaii*. In addition, *O. **exasperatus*** shows stronger spiral lirae on its ventral surface than does *O. savaii*. There are also differences in the anatomy: in the female, the proportions of the proximal and distal portions of the pallial common duct are different in the 2 taxa, and the male shows differences in proportions of penis thread to trunk, and in the slenderness or thickness of the penial trunk. Here are four areas of slight difference – shell shape, shell sculpture, male anatomy, and female anatomy – which together are sufficient to warrant separation of the 2 species.

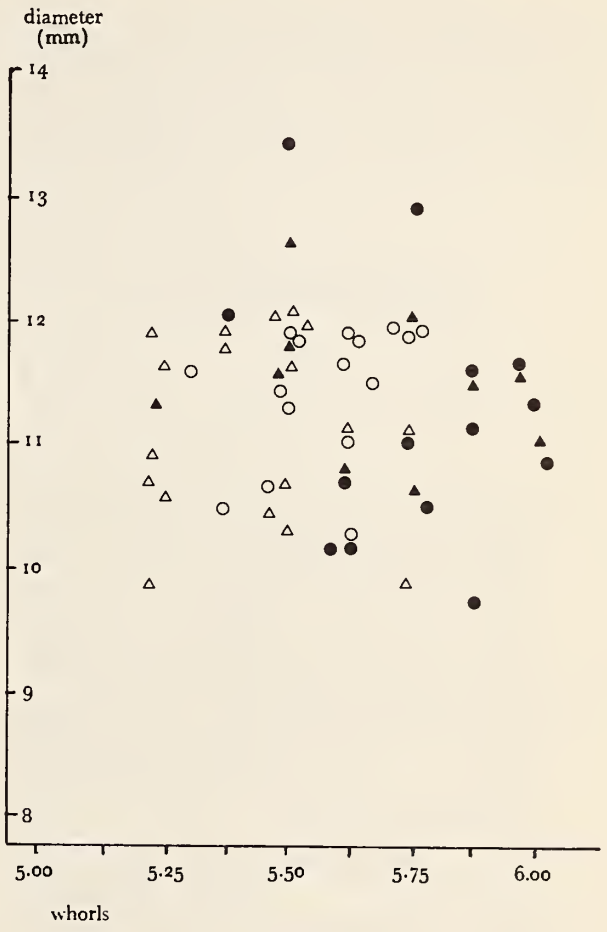


Figure 12

Relationship of whorl-count to diameter in *Ostodes savaii* and *Ostodes exasperatus*

△ – *Ostodes savaii*, male ○ – *Ostodes savaii*, female
▲ – *Ostodes exasperatus*, male ● – *O. exasperatus*, female

In the third example, the two forms of *Ostodes upolensis* were not deemed different enough to warrant their separation. As in the preceding example the differing appearances of the 2 types of shell are caused primarily by a single factor – the rate of decoiling. The size, the contour, and the width of the umbilicus are all determined in part by the rate of decoiling, and hence differences between them must be considered as having only a single cause. The anatomical differences observed in the 2 forms are in size only – not in shape or location – and are so

slight as to be statistically insignificant. There are no significant differences in sculpture. The single important difference between the forms – the rate of decoiling – was not thought sufficient to warrant separation of the taxon into 2 species, as it was unaccompanied by any significant differences in sculpture or anatomy.

4. SPECIES DIAGNOSES AND DISTRIBUTIONAL DATA

a. *Ostodes plicatus* (Gould, 1848)

(Figures 13a, b; 14b; 15c, d, e)

Cyclostoma plicatum Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 205 – Upolu; Gould, 1852, U. S. Expl. Exped., 12: 103–104: Gould, 1860, Atlas of Shells, U. S. Expl. Exped., plt. 8, figs. 118, 118a, 118b.

Cyclostoma apiae Récluz, 1851, Journ. de Conch., 2: 213, 214; plt. 6, figs. 10, 11 – Apia, Upolu.

Cyclophorus apiae (Récluz), Gray, 1852, Cat. Phan., pp. 57–58 – Pacific Islands, Upolu; Pfeiffer, 1852, Mon. Pneum., 1: 83 – Upolu.

Cyclostoma pulverulentum Philippi, 1854, *in* Pfeiffer, Conch. Cab., 1 [19(1)]: 301–302, plt. 40, figs. 13, 14 – Upolu.

Cyclophorus plicatus (Gould), Reeve, 1862, Conch. Icon., XIII: sp. 58, plt. 14, fig. 58.

Cyclophorus strigatus (Gould), Mousson, 1865, Journ. de Conch., 13: 179–180 – Upolu and Manua, Western Samoa – partly.

Cyclophorus (Ostodes) strigatus (Gould), Mousson, 1869, Journ. de Conch., 17: 350–351, Upolu, Savaii, Tutuila – partly.

Ostodes strigatus (Gould), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 147–148 – Upolu, Tutuila, Savaii – partly.

Ostodes plicatus (Gould), Kobelt, 1902, Das Tierreich, 16: 156, fig. 32 (p. 153) – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., 196: 15–17 – partly.

Diagnosis: Shell narrowly turbinate, height of adults 9.0–11.6 mm {10.45 mm}[1], diameter 8.8–10.6 mm {9.8 mm} with 5⅛–6 whorls {5⅝}. Whorls with rounded shoulders, suture slightly incised. Usually (85%) higher than wide; H/D ratio 0.92–1.19 {1.06}. (Juveniles, especially males, often wider than high.) Spire angle 70°–100° {81°}. Umbilicus deep, narrow, margin either smoothly rounded or pinched into an acute angle, but usually without a bordering rim. D/U ratio 2.69–4.46 {3.37}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus of adults approximately as thick as outer lip. Early whorls smooth. Body whorl with 4–12 {7.1} fine, evenly spaced spiral threads on upper palatal surface, 6–14 {9.3} spiral threads on lower palatal surface, crossing 15–27 {21.0} broad, strong, close-set radial plicae on upper surface, of which 13–23 {17.4} continue across rounded ventral surface and enter umbilicus. Color often salmon to rose pink on apex and spire, otherwise cream-color; body whorl nearly always cream-color. Periostracum thin, transparent, yellowish-brown, deciduous. Opercular types, A-1 and C-1.

Hypobranchial gland with moderately heavy posterior (transverse) portion, beginning well over to left side; anterior portion much reduced. Males have long-threaded penes without bulbs. Prostatic sac seldom present, "safety-valve" nearly always present; "valve" larger, sturdier, more obvious than in any other species. Female internal common duct very long (1.15 X diameter of bursa copulatrix). Pallial common duct very short, with copulatory pore immediately below mantle line, and entry of common duct into uterus immediately below pore, via slightly elevated oval papilla at 30° angle from long axis of uterus. Anus shows slight hypertrophy of upper margin. Vaginal orifice simply a round hole on the distal end of the uterus, equal in diameter to diameter of uterus. Terminal portions of both rectum and vagina bent sharply downward, at an angle approaching 90° in 80% of specimens seen. This bend is absolutely diagnostic of this species, as it occurs in no other. In the 20% without the bend, the anus points straight ahead, the uterus tapers to a point below the anus, and the vaginal orifice is a small hole on the ventral surface of the uterus.

Comparative remarks: Differing emphasis and distribution of sculptural elements on the body whorls are the chief conchological differences between *Ostodes plicatus* (Figure 13) and the most similar species, *O. gassiesi* (Clench, 1949: fig. 7a). Some of the material used by Clench in his work on *O. plicatus* was lent to me and proved to contain examples of both *O. plicatus* and *O. gassiesi*. In *O. plicatus,* the spiral threads are rather unobtrusive and evenly distributed over the entire height of the body whorl; in *O. gassiesi* they are clustered on the lower half, and are stronger. The radial plicae are much stronger in *O. plicatus;* they are narrower and much more numerous, and continue across the lower surface of the shell, which is smooth, or marked only by very faint spirals in *O. gassiesi*. The strong radial plicae also serve to differentiate *O. plicatus* from *O. strigatus, O. savaii, O. llanero,* and *O. exasperatus,* in all of which the radials are very weak or absent. In addition, the latter 4 species are usually as wide as or wider than tall, whereas *O. plicatus* is usually taller than wide. The sculpture of *O. plicatus* also differs considerably from the cross-hatched

[1] Data in braces { } represent the means of the preceding data

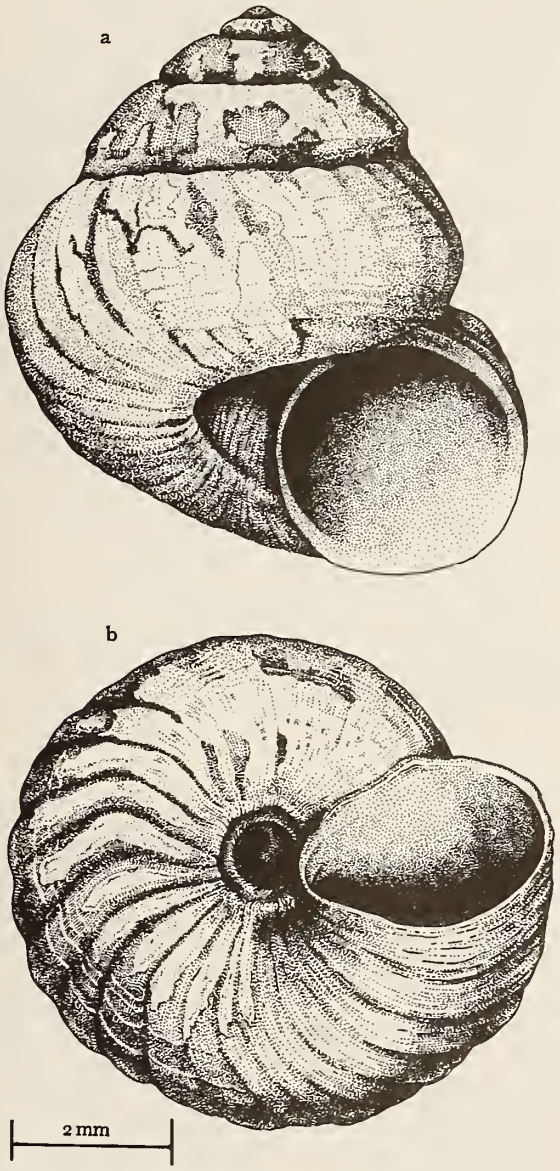


Figure 13

Ostodes plicatus

a – Shell seen from side b – shell seen from below

surface of *O. **reticulatus,*** which is a slightly smaller shell, wider than tall, with a much wider umbilicus. *Ostodes plicatus* is, of course, larger than *O. upolensis, O. adjunctus,* and *O. cookei,* and smaller than *O. garretti* and *O. tiara.*

In anatomy, although the reduced anterior portion of the hypobranchial gland is fairly distinctive, *Ostodes plicatus* is set off from other species of similar size chiefly by the reproductive systems. *Ostodes plicatus* males have longer penial threads, on the average, than do males of any species of comparable size except *O. strigatus* and *O. **reticulatus***. In the female reproductive systems, the downward bend of the terminal portions of rectum and vagina is unique to *O. plicatus;* in the unusual specimen in which the downward bend is lacking, the individual could still be distinguished from *O. **reticulatus*** and *O. strigatus* by the proportionate lengths of the common ducts. The interior common duct in *O. plicatus* is slightly longer than the diameter of its bursa copulatrix (as is that of *O. strigatus*), while that of *O. **reticulatus*** is less than one-half as long as its bursa is wide; the pallial common duct is very short in *O. plicatus,* but nearly 4 times the diameter of the copulatory pore in *O. **reticulatus,*** and 15 times the pore-diameter in *O. strigatus.*

Ostodes plicatus and *O. gassiesi* approach each other very closely in conchological characters. An empty shell, especially a worn shell, might well be impossible to assign with certainty to either species. The anatomy, however, is quite distinctive, and there should be no difficulty in identifying any whole specimen.

Range: Upolu, Western Samoa. Northeastern foothills, central uplands, and southern lowlands near coast. Altitude range 15 m – 750 m.

Material: Upolu: Station 2, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on right side of road in dense forest (6 specimens, FMNH 159173); Station 8, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on both sides of road in mixed to good forest (7 specimens, FMNH 170546, 159183, 159166); Station 9, Tafatafa, at 15 m elevation, in heavy forest (28 specimens, FMNH 152941, 159171): Station 18, at foot of Mount Solaua, at 180 – 240 m elevation, under *Ficus* tree in banana patch at edge of forest (59 specimens, FMNH 152894, 152842, 159163, 153107); Station 19, rim of Lake Lanuot'o crater, at 750 m elevation (1 specimen, FMNH 152836); Station 39, top of range above Solaua, at 600 m elevation, narrow ridge in heavy forest (6 specimens, FMNH 152588).

Totals: 107 specimens: 33 adult males, 24 adult females, 5 juvenile males, 4 juvenile females, 5 accidentally broken, 17 not sexed, 19 empty.

b. *Ostodes gassiesi* (Souverbie, 1858)

(Figures 1a, b; 14a; 15a, b)

Cyclostoma gassiesi Souverbie, 1858, Journ. de Conch., 7: 294, plt. 8, figs. 6 a, 6 b. Locality unknown.

Ostodes gassiesi (Souverbie), Kobelt, 1902, Das Tierreich, 16: 155 – Polynesia.

Ostodes plicatus (Gould), CLENCH, 1949, Bull. B. P. Bishop Mus., 196: 15–17, fig. 7 a – partly.

Diagnosis: Shell narrowly turbinate, height of adults 9.2–14.6 mm {11.3 mm}, diameter 9.0–12.2 mm {10.6 mm}, with 5⅛ to 6⅛ whorls {5⅝}. Whorls with rounded shoulders, suture slightly incised, ventral surface rounded. Usually (87%) higher than wide; H/D ratio 0.91–1.31 {1.07}. Spire angle 70°–100° {80°}. Umbilicus deep, narrow, margin usually smoothly rounded and without bordering rim. D/U ratio 2.75–4.61 {3.42}. Aperture round, holostomatous, slightly appressed to whorl above, parietal callus of adults not quite as thick as outer lip of aperture. Early whorls usually smooth. Body whorl with 3–9 {5.6} strong, narrow, spiral threads clustered on lower half of upper palatal surface, crossing 14–23 {17.6} broad radial plicae. At maturity, spiral threads fade out completely, radial plicae become broader, flatter, further apart and less definite, underlying numerous fine radial growth lines. Lower palatal surface usually smooth: occasionally shows faint traces of spiral lirae without relief. Rarely shows pink on apex and spire; generally cream-color; periostracum thin, brown, adherent. Opercular types A-1, B, C-1.

Juveniles differ from above in that they are usually wider than high (H/D ratio 0.79–1.07, mean 0.95), the body whorl has a sharply angled periphery, and the ventral surface is almost flat. Compare Figures 1a and 1b.

Hypobranchial gland large and prominent posteriorly, beginning well over to left side. Anterior portion tapers smoothly and is quite short, ending opposite middle of kidney. Males have short-threaded penes, often with subterminal bulb. Prostatic sac present frequently, "safety-valve" seldom. If "safety-valve" is present, it does not cross over the vas deferens to terminate behind and below anus, as usual, but is either very short, terminating on top of the vas, or if longer, runs down the medial aspect of the vas and terminates about midway between the anterior end of the prostate and the base of the penis. Female internal common duct short, only about ⅘ as long as bursa copulatrix is wide. Pallial common duct also short; copulatory pore down from mantle line only by its own diameter, with entry of common duct into uterus 1.5 pore diameters below pore. Common duct enters uterus via an elongate oval papilla, slightly elevated, its long axis at right angles to long axis of uterus. Anus a simple tube, pointing directly forward without hypertrophy of lips. Vaginal orifice a broad triangular slit, apex inward, its length 1.6 times the width of the uterus at the inner end of orifice.

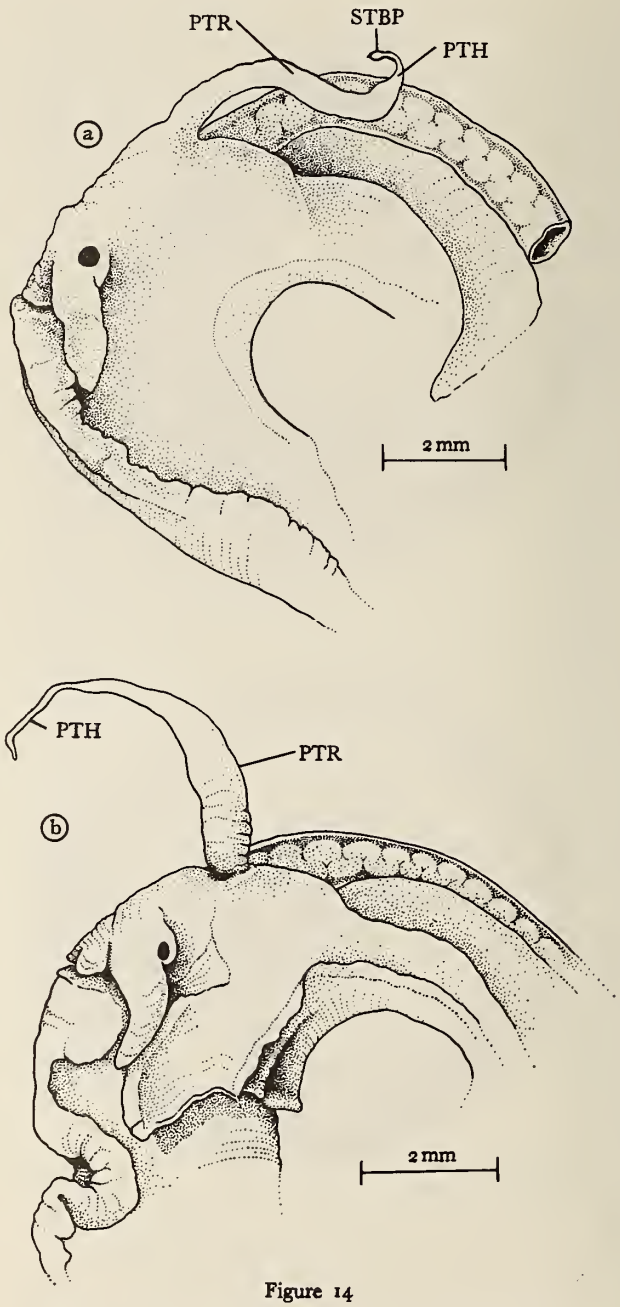


Figure 14

Males of (a) *Ostodes gassiesi* and (b) *Ostodes plicatus*

[for explanation of abbreviations see Appendix on foldout]

Comparative remarks: For the conchological differences between *Ostodes gassiesi* and the species most similar to it, *O. plicatus*, see comparative remarks under the latter species. *Ostodes gassiesi* differs from *O. savaii* in being narrower at a higher whorl count as well as in proportion to

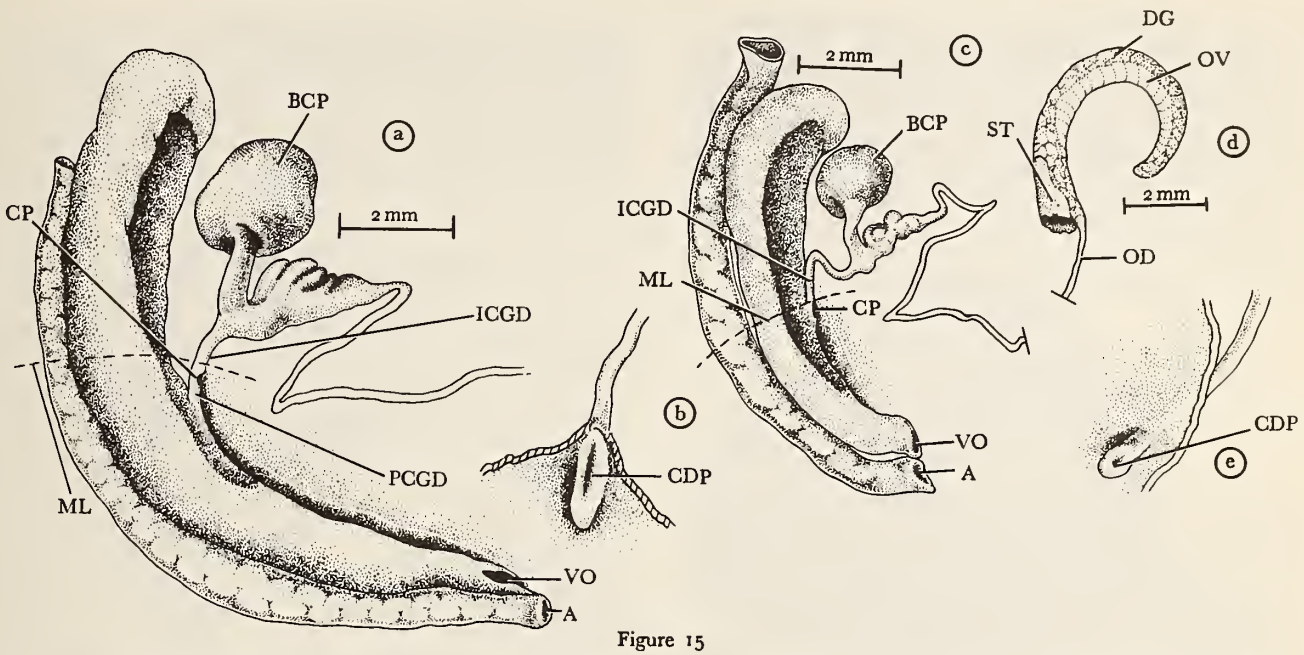


Figure 15

Female reproductive system of *Ostodes gassiesi* and *O. plicatus* a – *Ostodes gassiesi*; b – *O. gassiesi*, entrance of common genital duct into uterus; c – *O. plicatus*; d – *O. plicatus*, ovary; e – *O. plicatus*, entrance of common genital duct into uterus

[for explanation of abbreviations see Appendix on foldout]

its height, and by its strong radial sculpture, which is lacking in *O. savaii*. *Ostodes gassiesi* is also taller and narrower than *O. **reticulatus***, and taller than *O. strigatus*, with a more acutely angled spire and a much narrower umbilicus than either of the latter species.

As mentioned under *Ostodes plicatus*, that species and *O. gassiesi* are quite distinct anatomically. *Ostodes gassiesi* is closer anatomically to *O. savaii* than to any other of the middle-sized species, but is still distinct. In the male, both species are short-threaded, but *O. gassiesi* hardly ever has a "safety-valve," while that structure is present in more than ⅓ of the males of *O. savaii*. In the female reproductive system, both sections of the common duct are proportionately shorter in *O. gassiesi* than in *O. savaii;* the anal tip in *O. gassiesi* is a simple tube without hypertrophy, whereas in *O. savaii* there is considerable hypertrophy of the upper margin; and in *O. gassiesi* the upper lip of the vaginal orifice is longer than the lower lip, while the reverse is true in *O. savaii*.

Range: Upolu, southern and northeastern lowlands, western, central and northeastern foothills, central uplands. Altitude range, 15 m – 750 m. Savaii, eastern and southeastern lowlands, southern and southeastern foothills. Altitude range, 75 m – 450 m.

Material: Upolu: Station 2, 1.2 km above Afiamalu seismographic station, right of road, at 720 m elevation, in disturbed upland forest (10 specimens, FMNH 152705); Station 5, 1.6 km N of Tanumalala at 300 m elevation, in a thinned logging area with some bananas (9 specimens, FMNH 152765); Station 6, 1.6 km NW of Mt. Siga'ele, at 555 m – 570 m elevation, in forest patch in gully-pasture area (8 specimens, FMNH 152927); Station 7, foot of SE peak Tafua-Upolu at 450 m elevation, in forest part of transition zone above taro patch and newly cleared land (30 specimens, FMNH 152784, 152912); Station 8, 1.2 km above Afiamalu seismographic station, a wide area on both sides of road, including Station 2, 720 m elevation in disturbed upland forest (2 specimens, FMNH 170545, 152690); Station 9, Tafatafa, at 15 m elevation in heavy lowland forest (1 specimen, FMNH 152938); Station 10, Togitogiga, at 15 m elevation, in heavy lowland forest (1 specimen, FMNH 170535); Station 13, summit of pass to Fagaloa Bay, at 225 m elevation under a large mango tree in mixed foothill forest (1 specimen, FMNH 152666); Station 14, lower slope of SE peak Tafua-Upolu, at 390 m – 420 m elevation in disturbed to good foothill forest (9 specimens, FMNH 152753); Station 16, SE peak Tafua-Upolu at 480 m elevation, in undisturbed foothill forest (8 specimens, FMNH 159175); Station 17, top ridge SE peak Tafua-Upolu at 600 m elevation in disturbed foothill forest (2 specimens, FMNH 152774); Station 18, foot of Mt. Solaua, between 180 m – 240 m elevation, under a large *Ficus* tree in a banana patch at edge of lowland forest (3 specimens, FMNH 170551, 166215); Station 19, rim of Lake Lanuto'o crater at 750 m elevation, in heavy upland forest (18 specimens, FMNH 152809); Station 20, Lake Lanuto'o-Tapatapao trail, at 540 m elevation, in heavy foothill forest (41 specimens, FMNH 152795); Station 23, gully to foot of north side Mt. Siga'ele at 600 m – 645 m elevation in mixed to good foothill forest (8 specimens, FMNH 152606); Station 24, same gully as Station 23, but at 690 m elevation, in good foothill forest (1 specimen, FMNH 152905); Station 26, Afiamalu-Lake Lanuto'o track at 735 m – 750 m elevation, in good to excellent upland forest (36 specimens, FMNH 152670, 152719, 152721).

Savaii: Station 28, Vai'a'ata, near Vailoa, at 270 m elevation, on new road in tall open lowland bush (31 specimens, FMNH 152572, 152649); Station 30, about 8 km NW Vailoa at 180 m elevation, in heavy lowland forest (10 specimens, FMNH 170539); Station 36, about 12.8 km NW Vailoa at 270 m elevation in heavy foothill forest (8 specimens, FMNH 152634, 152642); Station 37, about 6.4 km W of Gatavai in dry stream bed at about 450 m elevation for 9.6 km in heavy foothill forest (6 specimens, FMNH 170541); Station 38, 800 m inland, 8 km E of Vailoa on road to Salelologa wharf, at less than 75 m elevation (1 specimen, FMNH 152631).

Totals: 244 specimens (188 from Upolu, 56 from Savaii); 86 adult females, 71 adult males, 19 juvenile females, 16 juvenile males, 28 not sexed, 24 empty.

c. *Ostodes reticulatus* Girardi, spec. nov.

(Figures 16a; 17a, b; 18a, b)

Diagnosis: Shell turbinate, height of adults 8.0–10.8 mm {9.2 mm}, diameter 9.1–11.2 mm {10.0 mm} with $5\frac{1}{8}$–$5\frac{5}{8}$ whorls {$5\frac{3}{8}$}. Whorls with rounded shoulders, dropping to flat, vertical area below periphery. Usually (92%) wider than high: H/D ratio 0.82–1.04 {0.93}. Spire angle 90°–100° {92°}. Umbilicus deep, very wide, often bordered by a rim formed by the innermost cord of spiral sculpture. D/U ratio 2.53–3.09 {2.78}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus of adults usually not quite as thick as outer lip. Spire smooth; sculpture usually badly worn on early whorls of adults. Body whorl with 4–8 {4.5} evenly spaced raised spiral cords on upper palatal surface, 6–11 {7.6} spiral cords on lower palatal surface, crossing 19–29 {23.0} radial cords on upper surface, of which 18–24 {20.6} continue on ventral surface. Both radial and spiral cords are of approximately the same height and width, and their crossing gives a reticulated surface effect, leaving square or oblong hollows, wider and taller than the width of the cords, between them. Color creamy white. Periostracum thin, light amber-brown; wears off raised cords but remains in hollows between them, where it is covered by accumulated environmental debris. Opercular type A-1.

Hypobranchial gland with reduced posterior portion; anterior portion long and dense, but quite slender. Males have long-threaded penes without bulbs. Both prostatic sac and "safety-valve" present. Female internal common duct moderately short – 0.43 times the diameter of the bursa copulatrix. Length of pallial common duct equal to approximately 4 times diameter of copulatory pore, with pore located slightly above mid-point of duct. Common duct enters uterus via an elevated papilla, narrowly heart-shaped with apex up, at right angles to long axis of uterus. Anus shows slight hypertrophy of upper margin. Vaginal orifice an oval hole on ventral aspect of uterus, its horizontal dimension being equal to $\frac{1}{3}$ the uterine diameter at posterior tip of orifice.

Comparative remarks: *Ostodes reticulatus* resembles *O. strigatus* more closely than it does any other of the mid-sized species of *Ostodes*. (See comparative remarks under

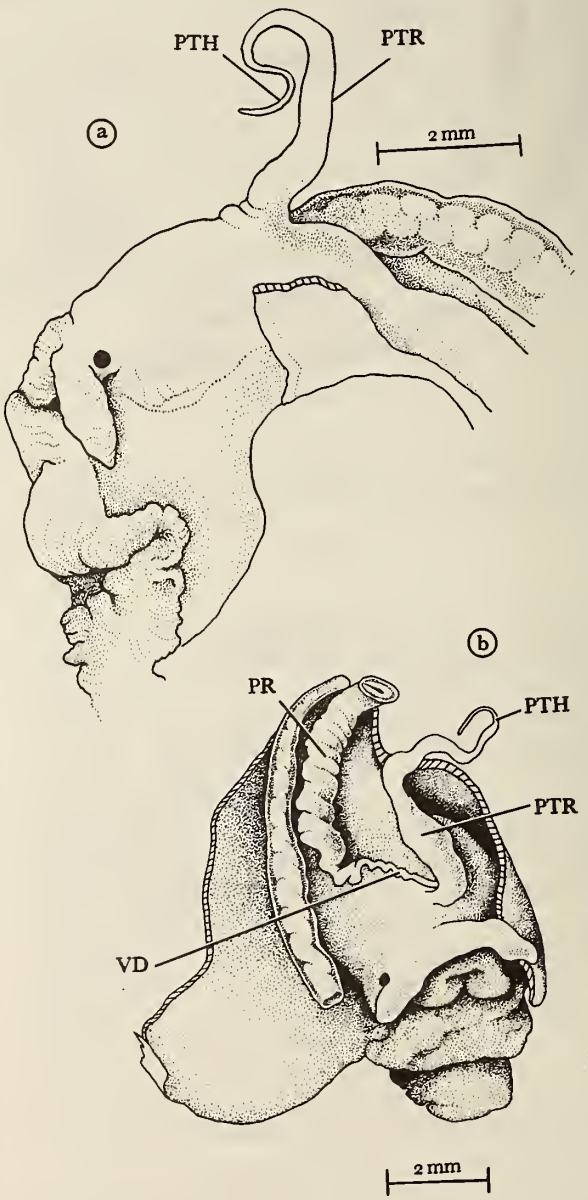


Figure 16

Males of (a) *Ostodes reticulatus* and (b) *Ostodes strigatus*
[for explanation of abbreviations see Appendix on foldout]

O. strigatus.) As regards the other species in the genus, the reticulated surface and the wide umbilicus are the most notable conchological characters separating *O. **reticulatus*** from *O. savaii*. *Ostodes savaii* lacks the radial threads that contribute to the reticulated surface of *O. **reticulatus***, has a narrower umbilicus, and is in addition a somewhat larger shell, and one that tends to have almost equal vertical and horizontal measurements, instead of being definitely wider than high, as is *O. **reticulatus***. Both *O. gassiesi* and *O. plicatus* are usually taller than they are wide, and have

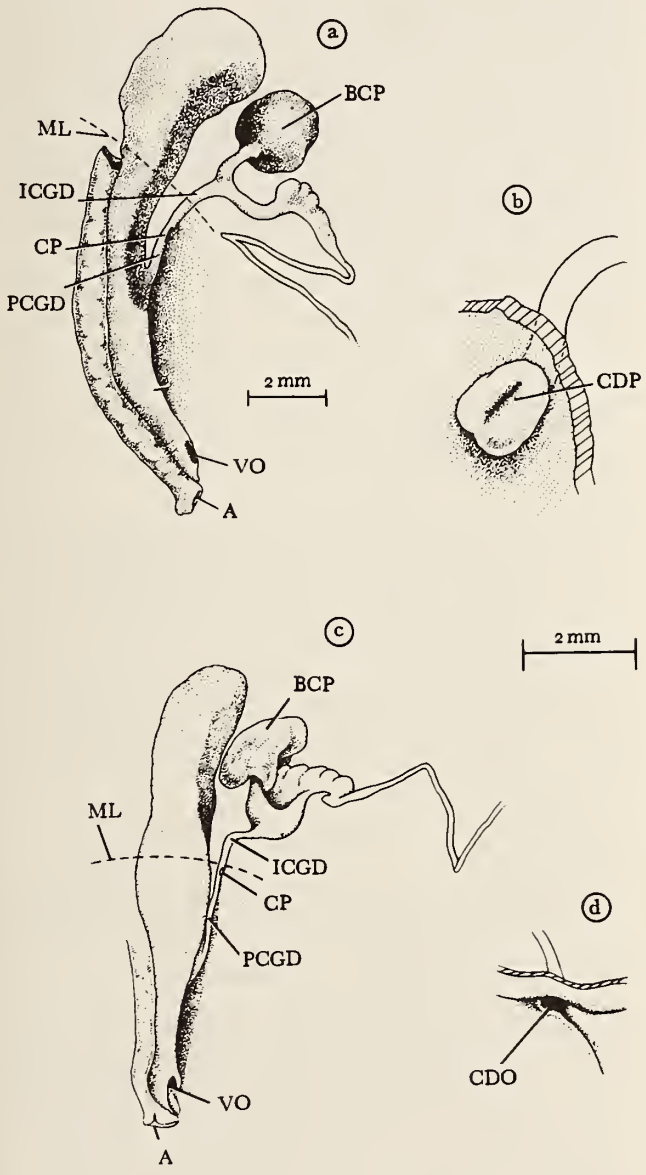


Figure 17

Female reproductive systems of *Ostodes **reticulatus*** and *O. strigatus*
a – *O. **reticulatus***; b – *O. **reticulatus***, entrance of common genital duct into uterus; c – *O. strigatus*; d – *O. strigatus*, entrance of common genital duct into uterus

[for explanation of abbreviations see Appendix on foldout]

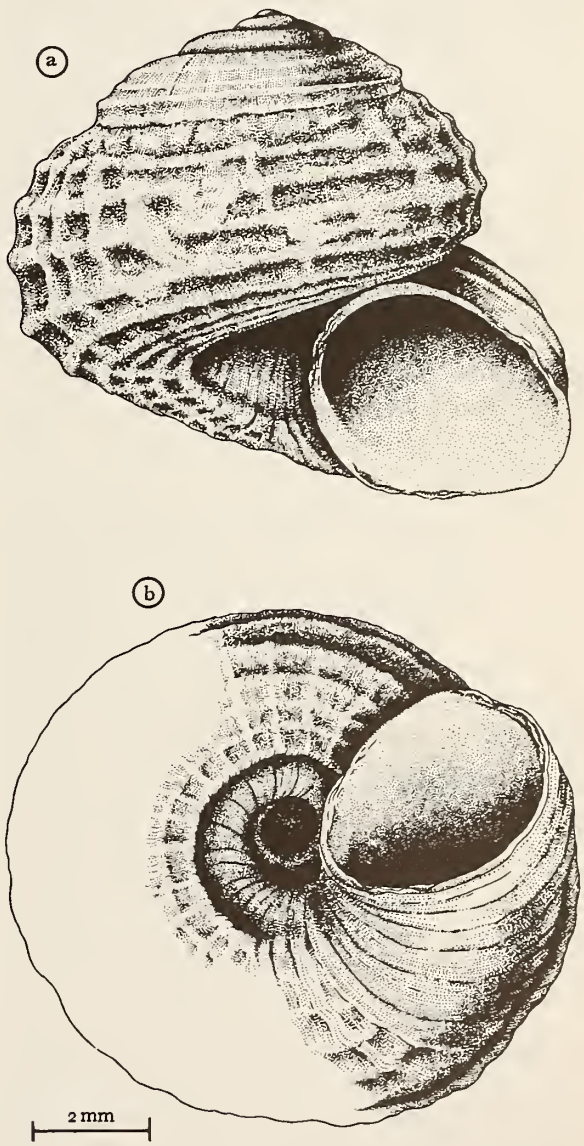


Figure 18

Ostodes reticulatus (holotype)
a – Shell seen from side b – shell seen from below

narrow umbilici. *Ostodes reticulatus* differs from *O. exasperatus* and *O. llanero* not only in its reticulated surface, but also in the shape of its whorls, which descend from the spire almost in a series of steps, whereas in the latter two species, the outline of the shell is a smooth, almost uninterrupted, convex curve.

Anatomically, *Ostodes reticulatus* seems more closely related to *O. strigatus* and *O. plicatus* than to the other middlesized species, but there should be no difficulty in differentiating among the three. For anatomical differences between *O. reticulatus* and *O. strigatus,* see under *O. strigatus.* The hypobranchial gland of *O. plicatus* is heavy posteriorly and reduced anteriorly, while that of *O. reticulatus* is reduced posteriorly but quite prominent anteriorly. Males of both species have similar penes (long threaded, without bulbs), but *O. reticulatus* is more apt to have a prostatic sac than is *O. plicatus,* and the "safety-valve" of the latter species is much more noticeable. In the female reproductive systems, *O. reticulatus* never has the downward bend of the terminal portions of rectum and vagina that characterizes *O. plicatus,* and the proportionate lengths of the common ducts are different, the internal duct being the longer in *O. plicatus,* the pallial duct being the longer in *O. reticulatus.*

Description of holotype: An adult female specimen, height, 9.3 mm; diameter, 10.2 mm; spire angle, 90°; H/D ratio, 0.91. Whorls 5⅛, decoiling at even moderate rate until near aperature, when rate increases so last 5 mm of body whorl are indented under periphery of penultimate whorl. Whorls with rounded shoulders but with narrow, flat, vertical area at lower margin of each, between lowest spiral thread and suture below. Nuclear whorl smooth; juvenile whorls somewhat worn. Upper palatal surface of body whorl with 25 radial cords, overlain by 4 spiral cords. Lower palatal surface with 19 radial and 6 spiral cords, of which the innermost forms a rim around the umbilicus. Intersecting radial and spiral cords produce a reticulated surface. Last 5 mm of body whorl with close-set radial lines of gerontic growth replacing major sculpture. Aperture round, holostomatous, diameter 3.9 mm, slightly appressed to whorl above; parietal callus as thick as outer lip. Umbilicus wide, deep, bounded by rim; D/U ratio 2.76. Deepest part of umbilicus filled with environmental debris. Shell white, translucent; periostracum extremely thin, pale amber color, very closely adherent; worn off raised portions of surface, present under organic debris in hollows. Operculum lost.

Collected by A. Solem and L. Price, on November 4, 1965, at Station 16, SE peak Tafua-Upolu, in undisturbed foothill forest at 480 m elevation, Upolu, W. Samoa. FMNH 170532.

Range: Upolu, W. Samoa, central foothills and uplands, northeastern foothills. Altitude range, 180–750 m.

Material: Upolu: Station 5, 1.6 km NW of Tanumalala, at 300 m elevation, in thinned logging area with some bananas (2 specimens, FMNH 152897); Station 6, 1.6 km NW Mt. Siga'ele, at 555–570 m elevation, in forest patch in gully-pasture area (2 specimens, FMNH 152928, 159186); Station 8, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on both sides of road in mixed to good forest (2 specimens, FMNH 159167, 159182); Station 16, SE peak Tafua-Upolu, at 480 m elevation, in undisturbed forest (7 specimens, FMNH 152757 (paratypes), 170532 (holotype)); Station 17, top ridge of SE peak Tafua-Upolu, at 600 m elevation, in disturbed forest (1 specimen, FMNH 159181); Station 18, foot of Mt. Solaua, at 180–240 m elevation, under a *Ficus* tree in banana patch at edge of forest (2 specimens, FMNH 159180, 166213); Station 23, gully to foot of N side Mt. Siga'ele, at 600–645 m elevation, in mixed to good forest (2 specimens, FMNH 159169); Station 24, N side Mt. Siga'ele, at 690 m elevation, in good forest (6 specimens, FMNH 159162); Station 26, Afiamalu-Lake Lanuto'o track at 735–750 m elevation, in good to excellent forest (1 specimen, FMNH 159178).

Total: 25 specimens; 7 adult males, 6 adult females, 5 juvenile males, 1 juvenile female, 3 not sexed, 3 empty.

d. *Ostodes strigatus* (Gould, 1848)

(Figures 16b, 17c, d)

Cyclostoma strigatum Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 204–205 – Upolu; Gould, 1852, U. S. Expl. Exped., 12: 102–103; Pfeiffer, 1853, Conch. Cab. 1 [19(1)]: 302–303, plt. 40, figs. 15, 16 – Upolu; Gould, 1860, Atlas of Shells, U. S. Expl. Exped., plt. 8, figs. 117, 117a, 117b.

Cyclophorus strigatus (Gould) Gray, 1852, Cat. Phan. p. 58 – Upolu; Pfeiffer, 1852, Mon. Pneum. 1: 83–84 – Upolu; Reeve, 1862, Conch. Icon., 13: sp. 77, plt. 17, fig. 77; Mousson, 1865, Journ. de Conch., 13: 179–180 – Upolu and Manua – partly.

Cyclostoma albida Hombron & Jacquinot, 1852–1854, Voyage au Pôle Sud, 5 [4(2)]: 50–51, plt. 12, figs. 25–28 – Samoa.

Cyclophorus (Ostodes) strigatus (Gould) Mousson, 1896, Journ. de Conch., 17: 350–351 – Upolu, Savaii, and Tutuila – partly.

Ostodes albidus (Hombron and Jacquinot) Kobelt, 1902, Das Tierreich, 16: 153 – Samoa.

Ostodes strigatus (Gould) Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 147–148 – Upolu, Tutuila, and Savaii – partly; Kobelt, 1902, Das Tierreich 16: 156 – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., 196: 13, figs. 4a, 4b – Tutuila: Laulii Valley at 30–150 m elevation; Fagatoga at 30–270 m elevation; foot of Mt. Tau at 24 m elevation; Logatala Ridge at 60 m elevation; Leone at 45 m elevation; Leone-Aolaoa Trail at 270–360 m elevation: Fagasa-Maupasaga Trail at 150 m elevation.

Diagnosis: Shell turbinate, height of adults 7.3–10.85 mm {9.32 mm}, diameter 8.6–11.6 mm {10.82 mm}, with 4⅝ to 5½ whorls {5⅛}. Sides of upper whorls somewhat flattened; body whorl with rounded shoulder. Suture in-

cised on approximately first 2 whorls; on later whorls, lowest spiral lira tends to overlie suture up to the start of the whorl-inset which marks maturity. Usually (93%) wider than high: H/D ratio 0.73–1.10 {0.91}. Spire angle 75°–100° {86°}. Ventral surface rounded. Umbilicus wide, deep, bordered by a protruding rim which is seen to be hollow in juveniles but becomes solid in adults; D/U ratio of adults 2.38–3.52 {2.89}. Aperture circular to (occasionally) sub-ovate with vertical diameter the greater; holostomatous, gently appressed to whorl above. Parietal callus approximately as thick as outer lip. Early whorls smooth. Body whorl with 3–7 {4.8} strong spiral cords, with which, in 42% of the shells examined, are interspersed from one to three slender spiral threads. In 37% of the juvenile shells examined, but only 19% of the adults, the spiral threads are beaded in such a way as to give the appearance of radial plicae crossing the spirals. There may be from 19–51 {adult: 30.7} such beads on the spiral cords of the body whorl, but only very rarely is there any trace of true raised radial sculptural elements between the spiral cords. In those few shells with true radial sculpture, the radial elements extend only from the suture down through the highest one or two spiral cords; they seldom reach the whorl shoulder, and never extend onto the ventral surface. Ventral surface usually (86%) smooth in adults. Remaining adults and about half the juveniles examined showed from 8–12 {8.9} ventral spirals, ranging from moderately prominent threads to barely perceptible lines without any relief at all. Since many more juveniles than adults showed some ventral spiral sculpture, its absence in adults may be due to wear. The absence of radial ventral sculpture, however, is a true shell character, not due to wear. Only one shell of 153 examined showed even the faintest trace of any radial sculptural elements on the ventral surface. Color light tan to cream-color, with an occasional pinkish spire. Periostracum thin, amber-colored; wears off raised spiral cords, but sometimes remains in valleys between cords, where it becomes covered by adherent environmental debris, giving the shell a spiral-striped appearance. Opercular types A-1, A-2, B, C-1, C-2, with half of the type B opercula (20% of the total number) being very concave (see p. 201).

Hypobranchial gland faint, tenuous; begins slightly to left of midline, turns and runs forward only to a point opposite the middle of the kidney. Males have penis with very long thread without bulb. In one male of 43 examined, penis was just to right of cephalic midline; penis on midline in all other specimens. Contrary to previous reports, all specimens seen had a closed vas deferens, not an open sperm groove. Vas deferens seems to be quite a long tube; it can be seen to be very convoluted as it runs beneath the integument from the prostate across to the penis. No "safety-valve" present, no prostatic sac; anterior end of prostate simply squared-off, without any constriction. Anterior medial corner makes a sort of flat flap, under which vas deferens crosses to penial base. Length of female internal common duct approximately equal to diameter of bursa copulatrix. Pallial common duct long; copulatory pore just below mantle line; entry of duct into uterus down 15 pore diameters. Common duct enters uterus via simple hole, partly hidden beneath soft, transverse fold of tissue, and opening into a sort of gutter or channel, which runs forward a short distance before fading into surrounding tissue. Anus with only very slight hypertrophy. Vaginal orifice a broad triangular slit, apex pointing inward, length approximately 1.3 times width of uterus at inner end of orifice.

Comparative remarks: *Ostodes strigatus* resembles *O. **reticulatus*** very closely. Although *O. strigatus* tends to have a lower whorl-count for its size than *O. **reticulatus,*** and a slightly more acutely-angled spire, shell sizes and proportions in the two species are almost identical. There are, however, considerable differences in sculpture. The spiral cords in *O. **reticulatus*** are evenly spaced and of uniform strength, and are crossed by radial cords of the same spacing and strength. Both spiral and radial elements continue strongly on the ventral surface of the shell. In *O. strigatus,* the spiral cords tend to be unevenly spaced and interspersed with much weaker threads. True radial sculpture is seldom found on the upper shell surface, and never on the ventral surface, which is usually entirely smooth.

The anatomical differences between *Ostodes strigatus* and *O. **reticulatus*** are much greater than the conchological differences. The hypobranchial gland of *O. strigatus* is much smaller and fainter. In the female, both internal and pallial common ducts are longer in *O. strigatus,* and the vaginal orifice is differently shaped and much larger than it is in *O. **reticulatus***. Males of both species have long-threaded, bulbless penes, but those of *O. strigatus* are longer (mean ratio, thread to trunk, $1/0.60 \pm 0.03$, compared to $1/0.91 \pm 0.15$) and a Student's *t* Test of the two ratios yields a *t* of 3.065 with 46 degrees of freedom, which indicates a probability of less than 0.01 that *O. strigatus* and *O. **reticulatus*** are the same.

Although Gould (1848, 1852, 1860) clearly differentiates between *Ostodes strigatus* and *O. plicatus,* later authors, notably Mousson (1865, 1869) confuse the two. *Ostodes plicatus* is taller than it is wide, with radial sculpture predominant; *O. strigatus* is wider than it is tall, with almost exclusively spiral sculpture. Students' *t* Tests comparing male and female heights and diameters of *O. strigatus* and *O. plicatus* indicate a probability of less than 0.001 that these two species are the same.

Similar *t* tests of heights and diameters between *Ostodes strigatus* and the 3 other mid-sized species of *Ostodes* indicate that there is less than 0.01 probability of identity between *O. strigatus* and *O. gassiesi,* and less than 0.001 probability of identity between *O. strigatus* and *O. savaii;* in addition, *O. strigatus* has fewer whorls and a wider umbilicus than either *O. gassiesi* or *O. savaii.* The probability of identity between *O. strigatus* and *O. **exasperatus*** is approximately 0.015 as regards shell height and diameter, with *O. strigatus* a smaller shell with fewer whorls, that is much less likely to have spiral sculpture ventrally. Anatomically, both *O. gassiesi* and *O. savaii* usually have short-threaded penes, often with sub-terminal bulbs; *O. strigatus* has a very long-threaded, bulbless penis. The chief anatomical difference between *O. strigatus* and *O. **exasperatus*** is in the female genitalia, with the copulatory pore of *O. strigatus* much closer to the mantle line, and the pallial common duct about 3 times as long as that of *O. **exasperatus.***

Comparison of juvenile shells of *Ostodes strigatus* with the available juveniles of *O. **llanero*** reveals that *O. strigatus* is taller, with a more acute spire angle and a narrower umbilicus. *Ostodes strigatus* is, of course, larger than *O. upolensis, O. adjunctus,* and *O. cookei,* and smaller than *O. tiara* and *O. garretti.*

Range: Tutuila, American Samoa; western portion of island: center and south-east edge of central plateau, extreme southern coast, mountain slope near (just south of) Pago Pago. Altitude range, 60–390 m.

Materials: Tutuila. Station AS-6; central plateau above Aolaoufou, 21 km SW Pago Pago, 360–390 m elevation (74 specimens, FMNH 181051/N). Station AS-10; middle slopes NE side Matafao Peak, reservoir track, behind Pago Pago, in dense forest (33 specimens, FMNH 181083/N). Station AS-19; upper slopes Olotele Mt., edge of central plateau, at 270–330 m elevation, SW of Pago Pago (26 specimens, FMNH 181151/N). Station AS-20; seaward slopes Fagatele Crater, 19 km SW Pago Pago, at 60 m elevation (20 specimens, FMNH 181157/N).

Totals: 153 specimens: 44 adult males, 40 adult females, 20 juvenile males, 17 juvenile females, 32 not sexed.

e. *Ostodes savaii* Clench, 1949

(Figures 19a; 20a, b, c)

Ostodes savaii Clench, 1949, Bull. B. P. Bishop Mus., 196: 14, 15, figs. 5, 6 – Savaii: Salailua, at 90–180 m elevation; Matavanu, ±900 m; Siuvao-Auala (1.6–6.4 km inland) at 150–600 m elevation.

Diagnosis: Shell turbinate, height of adults 7.6–13.6 mm {10.7 mm}, diameter 8.2–13.0 mm {11.0 mm} with $5\frac{1}{8}$–$5\frac{7}{8}$ whorls {$5\frac{1}{2}$}. Whorls with rounded shoulders, suture well defined. Tends to be approximately equal in height and width, H/D ratio 0.79–1.19 {0.98}. Spire angle 70°–100° {86°}. Umbilicus deep, narrow; inner edge of final whorl often sharply angled at umbilical border, but seldom having a rim. D/U ratio 2.32–4.40 {3.18}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus not as thick as outer lip of aperture. Early whorls usually smooth. Body whorl with 4–12 {5.8} fine but strong spiral threads on upper palatal surface, crossing 11–26 {19.9} broad, rather low and poorly-defined radial plicae. Lower palatal surface with 4–17 {10.8} spiral threads or lines, usually not as prominent as those on upper surface, often just lines, without any relief. Radial plicae hardly indicated at all on lower surface. Color creamy; periostracum thin, brown, deciduous. Opercular types A-1, B, C-1, C-2.

Hypobranchial gland with quite prominent posterior portion: anterior portion reduced in width and thickness, but runs almost $\frac{2}{3}$ of way from mantle line to anterior mantle margin. Males mostly (86.5%) with short-threaded penes; about half have sub-terminal bulbs. Most have prostatic sacs, but only about $\frac{1}{3}$ have "safety-valves." Female anterior common duct quite long, being slightly longer than bursa copulatrix is wide. Pallial common duct of moderate length, copulatory pore being anterior to mantle line by its own diameter, with entrance into uterus 4 pore-diameters below pore. Entrance of common duct into uterus via an elevated, round papilla. Anus shows considerable hypertrophy of upper margin, only slight hypertrophy of lower margin. Vaginal orifice a narrow triangular slit, apex in, its length equal to 2.1 X diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes savaii* resembles *O. **exasperatus*** very closely; the differences and similarities between these two species are discussed under comparative remarks for *O. **exasperatus.*** *Ostodes savaii* differs from *O. gassiesi* and *O. plicatus* in proportion, being wider at a lower whorl count as well as in proportion to its height. In addition, both *O. gassiesi* and *O. plicatus* have strong radial sculpture which is lacking in *O. savaii. Ostodes savaii* is a larger shell, with more whorls and a narrower umbilicus, than *O. strigatus. Ostodes **reticulatus*** is a smaller shell than *O. savaii,* and has a reticulated surface quite unlike that of the larger species.

The anatomical differences between *Ostodes savaii* and *O. **exasperatus,** O. strigatus* and *O. gassiesi* are discussed under the latter 3 species.

Range: Upolu, Western Samoa: northeastern, southern, and extreme southeastern lowlands; western, west-central, central and north-central foothills; central uplands. Altitude range, 3–750 m. Savaii, Western Samoa: eastern, southeastern and southwestern lowlands; western, south-

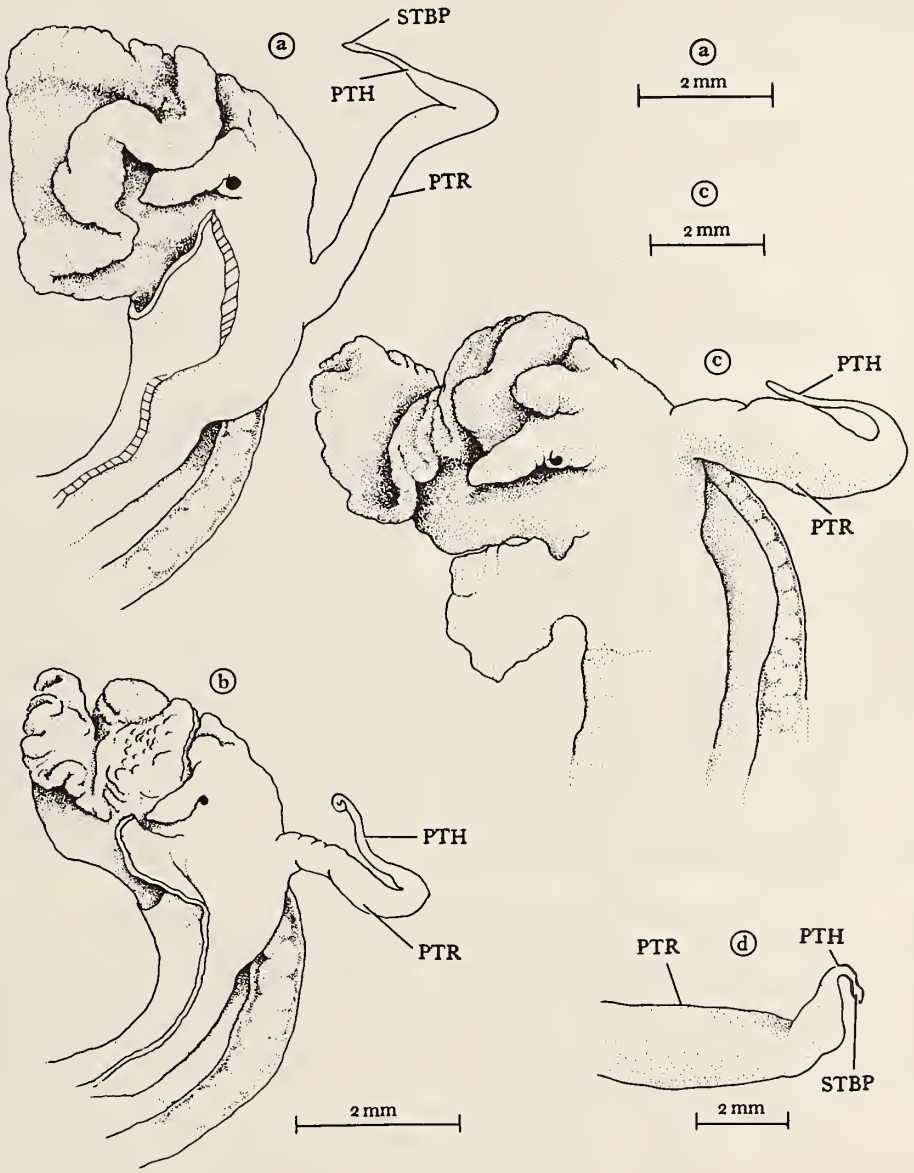


Figure 19

Males of *Ostodes savaii, Ostodes llanero* and *Ostodes exasperatus*
a – *O. savaii*; b – *O. llanero*; c – *O. exasperatus*, male from Upolu; d – O. *exasperatus*, type of penis found in Savaii population

[for explanation of abbreviations see Appendix on foldout]

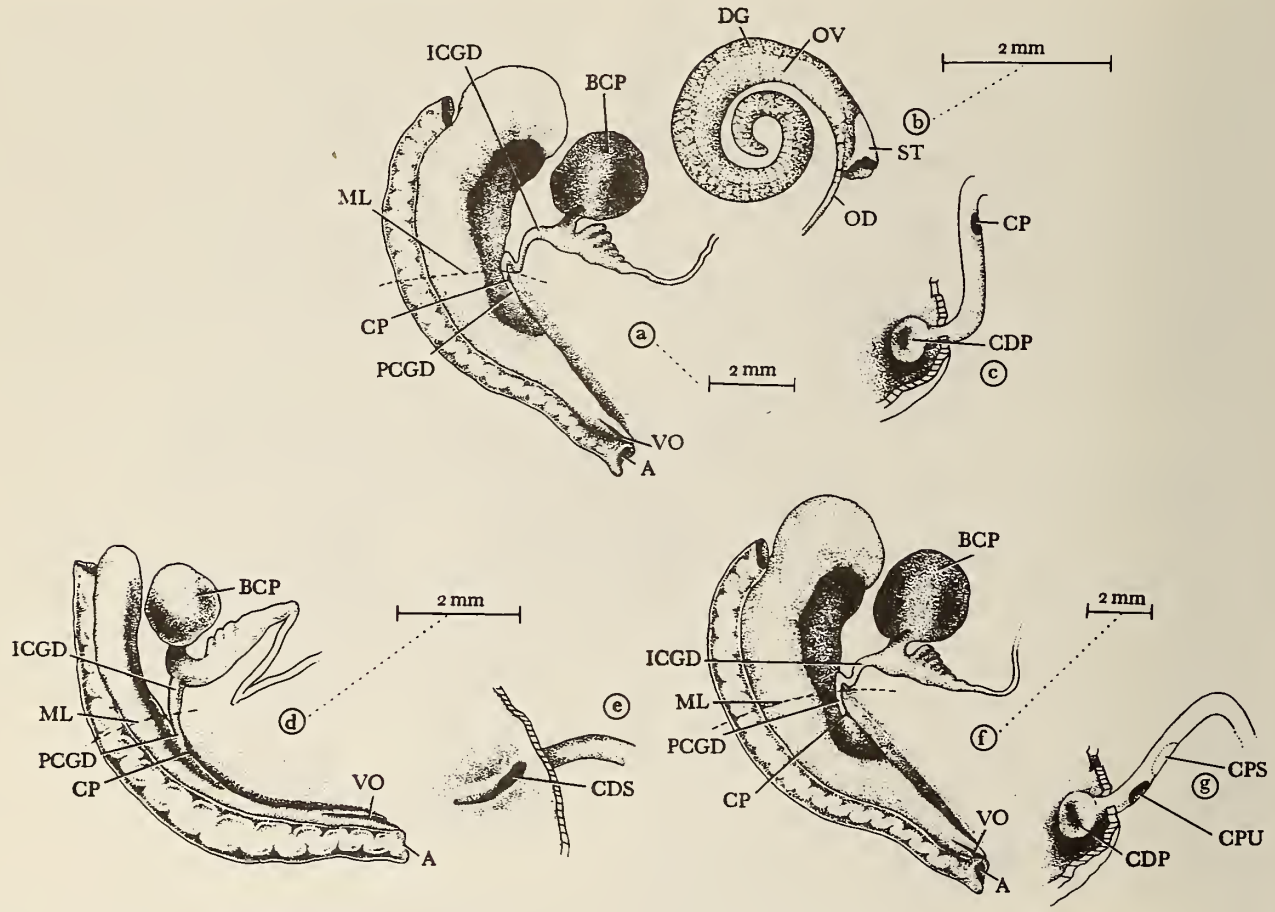


Figure 20

Female reproductive system of *Ostodes savaii*, *Ostodes llanero* and *Ostodes exasperatus*

a – *O. savaii*; b – *O. savaii*, ovary; c – *O. savaii*, entrance of common genital duct into uterus; d – *O. llanero*; e – *O. llanero*, entrance of common genital duct into uterus; f – *O. exasperatus*; g – *O. exasperatus*, entrance of common genital duct into uterus, and position of copulatory pore in both populations

[for explanation of abbreviations see Appendix on foldout]

Explanation of Figures *43* to *48*

Figure *43*: *Ostodes llanero*, central, lateral, and inner marginal teeth × 736

Figure *44*: *Ostodes llanero*, outer marginal teeth, showing foramina × 786

Figure *45*: *Gonatorhaphe* sp., radula torn, showing base of central tooth and shank of lateral tooth × 235

Figure *46*: *Gonatorhaphe* sp., radula partly closed, showing edge of membrane and foramina in outer marginal teeth × 344

Figure *47*: *Gassiesia* sp., central tooth and tricuspid lateral teeth × 548

Figure *48*: *Gassiesia* sp., radula partly closed, showing outer marginal teeth × 235


43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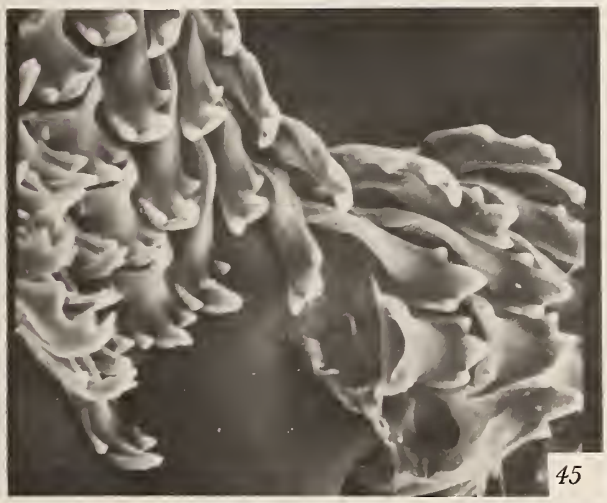
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47


48

ern and southeastern foothills. Altitude range, 150–450 m.

Material: Upolu: Station 2, 1200 m above Afiamalu seismographic station, on right of road at 750 m elevation in disturbed upland forest (5 specimens, FMNH 159174); Station 6, 1.6 km NW of Mt. Siga'ele at 555 m elevation, in a forest patch in a gully-pasture area (1 specimen, FMNH 159187); Station 7, foot SE peak Tafua-Upolu at 360 m elevation in forest part of transition zone above taro patch and newly cleared land (3 specimens, FMNH 159177); Station 8, 1.2 km above Afiamalu seismographic station, in wide area on both sides of road, including Station 2, at 720 m elevation in mixed to good upland forest (12 specimens, FMNH 170538, 152875, 159168); Station 9, Tafatafa, in heavy lowland forest at 15 m elevation (3 specimens, FMNH 170537, 170533, 159172); Station 10, Togitogiga, two logging roads toward ocean, at 15 m elevation, in thinned lowland forest (1 specimen, FMNH 170543); Station 16, SE peak Tafua-Upolu at 480 m elevation in undisturbed foothill forest (1 specimen, FMNH 159176); Station 18, foot of Mt. Solaua between 180–240 m elevation, under a large *Ficus* tree in banana patch at edge of forest (6 specimens, FMNH 153020, 159164, 159165, 166214); Station 20, Lake Lanuto'o-Tapatapao trail, at 540 m elevation in heavy foothill forest (1 specimen, FMNH 170534); Station 24, N side of Mt. Siga'ele at 690 m elevation, in good foothill forest (1 specimen, FMNH 170542); Station 25, cliffs at Tuiolemu at 3–150 m elevation in mixed to good lowland forest (8 specimens, FMNH 153108, 153432); Station 26, Afiamalu-L. Lanuto'o track at 735–750 m elevation in good to excellent upland forest (9 specimens, FMNH 170544, 170547, 170536, 159178, 159179, 159184, 159185); Station 40, summit of Mt. Vaea, near tomb of Robert Louis Stevenson, at 420 m elevation in much disturbed foothill forest (26 specimens, FMNH 152582).

Savaii: Station 28, Vai'a'ata, near Vailoa, at 270 m elevation, on a new road in tall open lowland bush (19 specimens, FMNH 170548, 170540); Station 30, about 8 km NW of Vailoa at 180 m elevation in heavy lowland forest (17 specimens, FMNH 153001, 153008); Station 31, 2 km in from Salilua, 41.6 km W of Vailoa, at 150 m elevation, in heavy lowland forest (38 specimens, FMNH 152741, 152791); Station 32, up a survey track at 450 m elevation, approximately 8 km inland from Asau in open foothill forest (26 specimens, FMNH 152526); Station 36, about 12.8 km NW of Vailoa, at 270 m elevation, in heavy foothill forest (1 specimen, FMNH 170549); Station 37, about 1.6 km W of Gatavai, at about 450 m elevation, in dry stream bed for 10 km in heavy foothill forest (10 specimens, FMNH 152560).

Totals: 188 specimens (111 from Savaii, 77 from Upolu); 58 adult males, 52 adult females, 11 juvenile males, 16 juvenile females; 22 not sexed, 18 empty.

f. *Ostodes exasperatus* Girardi, spec. nov.

(Figures 19c, d; 20f, g; 21a, b)

Diagnosis: Shell turbinate, height of adults 8.6–12.9 mm {10.4 mm}, diameter 9.8–13.4 mm {11.3 mm}, with $5\frac{1}{4}$–$6\frac{1}{8}$ whorls {$5\frac{3}{4}$}. Silhouette smoothly convex, suture not incised. Usually (88%) wider than high; H/D ratio 0.81–1.00 {0.92}. Spire angle 80°–105° {90°}. Umbilicus wide, deep, usually (67%) bounded by a rim formed by innermost spiral cord, D/U ratio 2.36–3.85 {2.98}. Aperture sub-circular, slightly compressed vertically, very slightly appressed to whorl above. Parietal callus not as thick as outer lip. Apex and early whorls usually smooth. Body whorl with 4–7 {5.5} strong spiral cords on upper palatal surface, 6–20 {12.0} spiral cords on lower palatal surface. Only one shell of 24 adults examined showed any trace of radial sculpture except fine growth lines. Color creamy white. Periostracum thin, brown, deciduous. Opercular types A-1, A-2, B, C-1, C-2.

Hypobranchial gland narrow and elongate: runs nearly to front margin of mantle cavity. Males from Upolu have long-threaded penes without bulbs; those from Savaii mostly have short-threaded penes with bulbs. In both populations prostatic sacs and "safety-valves" are unusual. Female internal common duct very long (approximately equal to the diameter of the bursa copulatrix). Pallial common duct also long; copulatory pore anterior to mantle line by 3.5 times its own diameter. In females from Upolu, entrance of common duct into uterus is immediately below copulatory pore; in Savaii females, the entrance is approximately 2 pore diameters below the pore itself. This is the only difference in the female systems between the 2 populations. Entrance of common duct into uterus is via an elevated round papilla. Anus points directly forward, shows considerable hypertrophy of upper margin, slight hypertrophy lower margin. Vaginal orifice a narrowly triangular slit, apex inward, on the medioventral aspect of the uterus. Length of vaginal orifice approximately 1.6 times uterine diameter at inner end of orifice.

Comparative remarks: *Ostodes **exasperatus*** is very similar to both *O. savaii* and *O. **llanero***. For the differences between *O. **exasperatus*** and *O. **llanero***, see comparative remarks under the latter species. The principal conchological difference between *O. **exasperatus*** and *O. savaii* is the contour of the shell. The spire of *O. savaii* descends with a progressively increasing rate of decoiling; although the early whorls present a fairly even contour, there is a definite "step" effect between the penultimate whorl and the body whorl, with an almost vertical drop from the periphery of the penultimate whorl to the suture below. In *O. **exasperatus***, the rate of decoiling is slower and more even, with the periphery of each whorl slightly overlying the suture. In addition, *O. **exasperatus*** averages very slightly shorter and wider than *O. savaii*, its umbilicus is slightly wider in proportion to the diameter of the shell, and it has a slightly higher whorl count for its size than does *O. savaii*. For differences between *O. **exasperatus*** and *O. strigatus*, see under the latter species.

Anatomically, *Ostodes **exasperatus*** differs considerably from *O. **llanero***, as discussed under that species. The differences between *O. **exasperatus*** and *O. savaii* are smaller, but consistent. In the female, the difference is in the length and proportions of the pallial common duct. In *O. **exasperatus***, the portion of the pallial common duct above the copulatory pore is considerably longer than that below the pore; in *O. savaii*, the reverse is true. In the male, *O. savaii* is much more apt to have a prostatic sac than is *O. **exasperatus***, and slightly more apt to have a "safety-valve." The penial trunk of *O. savaii* is slender

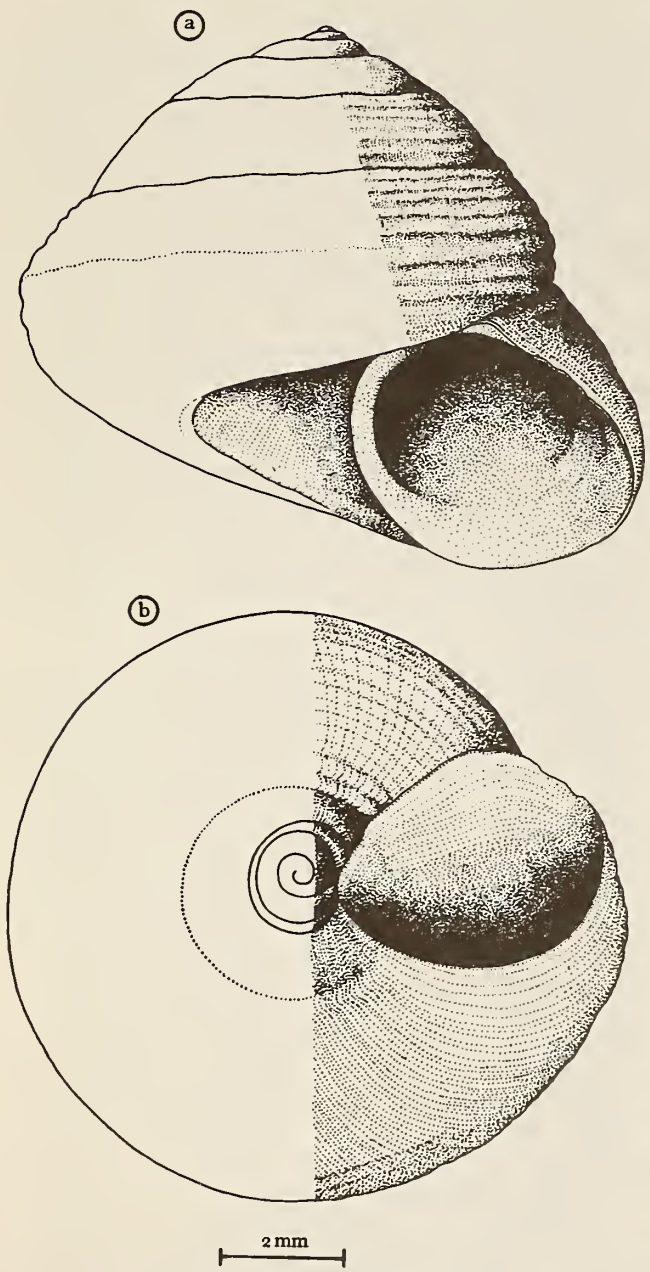


Figure 21

Ostodes exasperatus (holotype)

a – Shell seen from side b – shell seen from below

in proportion to its length; that of *O. exasperatus* is thick and heavy. On Upolu, where the 2 species may be sympatric, 86% of *O. savaii* males have short-threaded penes; all *O. exasperatus* males are long-threaded. On Savaii, where the 2 species are definitely allopatric, they are both mostly short-threaded.

Description of holotype: A young adult male, height 10.2 mm, diameter 11.5 mm, spire angle 85°, H/D ratio 0.88. Whorls $5\frac{7}{8}$, decoiling slowly until the last 4 mm of body whorl, when rate increases so that terminal portion of whorl is slightly inset. Turbinate, with slightly indented suture, for first $2\frac{1}{2}$ whorls. Thereafter suture not indented; periphery of each whorl over-lies whorl below very closely, producing a smoothly convex silhouette. First $2\frac{1}{2}$ whorls smooth; succeeding whorls progressively more sculptured. Body whorl with 6 strong, narrow, raised spiral cords on upper palatal surface, 15 somewhat less emphatic spiral cords on lower palatal surface. Innermost spiral cord of ventral surface forms rim of umbilicus, which is open to nuclear whorl. D/U ratio, 2.74. Major sculpture replaced by fine radial growth lines on last 4 mm of body whorl. Aperture sub-circular, diameter 4.5 mm, vertically compressed and slightly appressed to whorl above. Parietal callus thin. Creamy white with brown, deciduous periostracum. Operculum type C-2.

Collected by L. Price on November 20, 1965 at Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m elevation, in light upland forest, Savaii, W. Samoa. FMNH 170530.

Range: Savaii, Western Samoa, northwestern uplands. Upolu, W. Samoa, locality unknown.

Material: Upolu; Station unknown (12 specimens, FMNH 153820). Savaii: Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m elevation, in light upland forest (17 specimens, FMNH 170531).

Totals: 29 specimens, (12 from Upolu, 17 from Savaii); 14 adult females, 2 juvenile females, 10 adult males, 3 juvenile males.

Remarks: The 2 populations of this species, from the 2 islands, are not exactly alike. They are definitely closer to each other than either one is to anything else, therefore they are kept together. As has been mentioned above, the Upolu population of *Ostodes exasperatus* reverses the usual condition of sexual dimorphism in the genus by having males that are bigger than females; the Savaii population conforms to the more normal state of having bigger females.

g. *Ostodes llanero* Girardi, spec. nov.

(Figures 22a, b; 19b; 20d, e)

Diagnosis: Shell broadly turbinate; height of juveniles 6.6–6.9 mm {6.7 mm}, diameter 9.0–9.8 mm {9.44 mm}

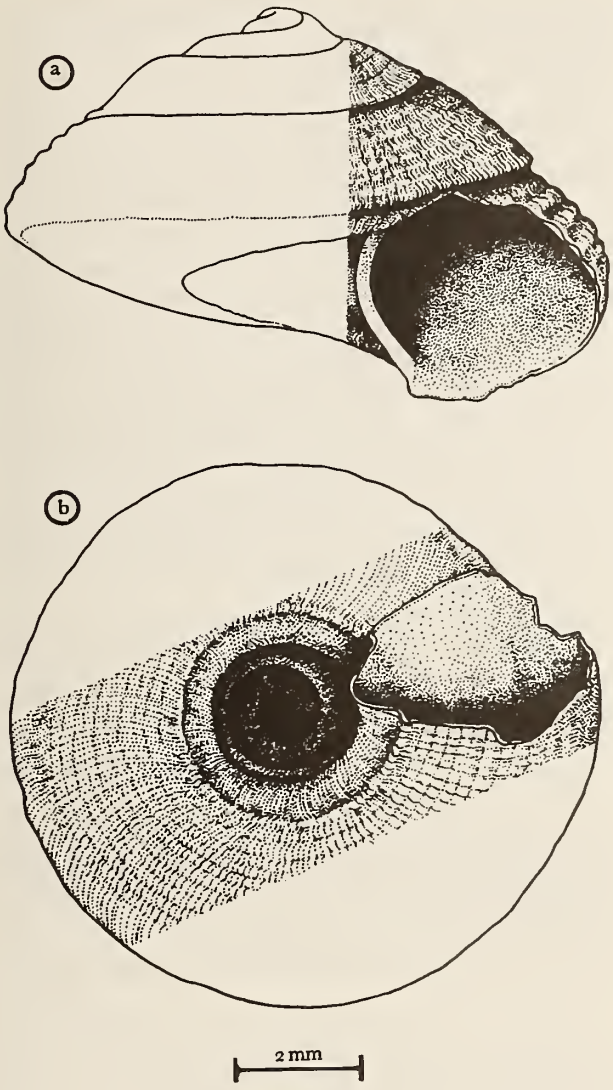


Figure 22

Ostodes llanero (holotype)

a – Shell seen from side b – shell seen from below

with 5–5⅛ whorls. Whorls very slightly convex, almost flat-sided, suture covered by lower margin of whorl above. Body whorl with rounded shoulder. Always wider than high; H/D ratio 0.64–0.74 {0.70}. Spire angle 100°–120° {110°}. Umbilicus very wide, deep, bounded by rim, D/U ratio 1.99–2.61 {2.37}. Aperture sub-circular, slightly compressed, appressed to whorl above, and with extension into hollow peri-umbilical rim. Parietal callus very thin. Apex smooth, early whorls usually worn; body whorl with 5–7 {6.0} close-set spiral lirae on upper palatal surface, 12–15 {13.3} finer spiral traces on lower palatal surface. These strong spirals crossed by numerous exceedingly fine radial threads. Shell thin, fragile, white, almost transparent; periostracum very thin, brown, deciduous. Opercular type C-2.

Hypobranchial gland not well developed in these juvenile specimens. Transverse (posterior) portion begins only slightly to left of midline of mantle; anterior portion also very short. Male has long-threaded penis without bulb; no prostatic sac, no "safety-valve." Female internal common duct moderately short, 0.47 times the diameter of the bursa copulatrix. Pallial common duct very short, with copulatory pore anterior to mantle line by approximately twice its own diameter, and entry of common duct into uterus immediately below copulatory pore, via a vertical slit, slightly wider at top than at bottom, at right angles to long axis of uterus. No papilla, no hypertrophy of edges of slit. Anus shows very slight hypertrophy of both upper and lower edges. Vaginal orifice a very long slit in medial aspect of uterus. Length of slit 4–4.5 times diameter of uterus at inner end of slit.

Comparative remarks: *Ostodes llanero* is a sibling species of *O. exasperatus*. The only differences between juvenile shells of the 2 species (no adults of *O. llanero* were seen) are the spire angle, which averages 21° wider in *O. llanero*, and the D/U ratio, which averages 0.57 smaller. (Table 6) Otherwise the shells are virtually identical. The anatomy, however, is quite different. Males of *O. exasperatus* from Savaii tend to have short-threaded penes with sub-terminal bulbs; the single male seen of *O. llanero* had a long thread without a bulb. The greatest difference

Table 6

Differences between *Ostodes llanero* and *Ostodes exasperatus* (juveniles, mixed sex)

	Spire angle			D/U ratio		
	N	Range	Mean	N	Range	Mean
Ostodes exasperatus	5	85° - 90°	89°	5	2.52 - 3.30	2.94
Ostodes llanero	2	100° - 120°	110°	3	1.99 - 2.61	2.37

between the two species is in the female reproductive system. Each section of the common duct in *O. **exasperatus*** is approximately twice the length of the corresponding section in *O. **llanero***, each measured in relation to its own bursa copulatrix and copulatory pore. The vaginal orifice in *O. **llanero*** is 4–4.5 times the width of the uterus at the inner end of the orifice, whereas in *O. **exasperatus***, the vaginal orifice is only 1.6 times the uterine width. Also, in *O. **llanero***, the upper lip of the vagina extends farther forward than does the lower lip, while in *O. **exasperatus***, the lower lip is the longer of the two.

Although its smoothly convex outline, smaller size, and lack of strong radial sculpture set *O. **llanero*** apart from the other mid-sized species of *Ostodes*, the most striking difference is the very wide umbilicus. Although there is some overlap of ranges, at 2.37, the mean D/U ratio of *O. **llanero*** is considerably lower than that of any other mid-sized species. (Figure 23)

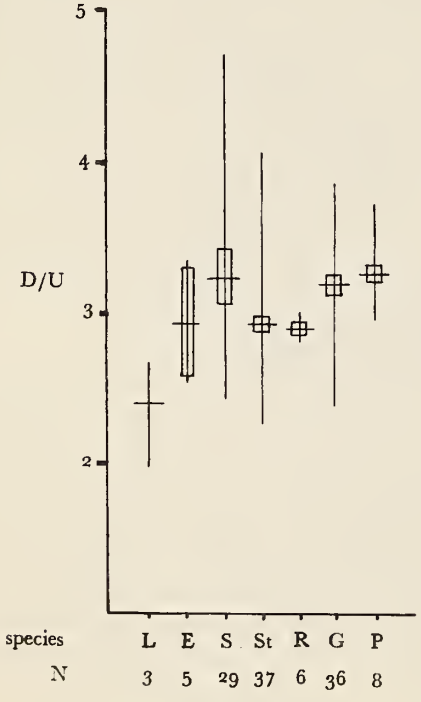


Figure 23

Comparison of D/U ratios of mixed-sex juveniles of 7 mid-sized species of *Ostodes*

E – *O. exasperatus*; G – *O. garretti*; L – *O. llanero*; P – *O. plicatus*; R – *O. reticulatus*; S – *O. savaii*; St – *O. strigatus* Vertical line – range of measurements; horizontal line – mean; box – two standard errors on either side of mean

Description of holotype: A juvenile female, height 6.6 mm, diameter 9.78 mm, very broadly turbinate, spire angle 120°, H/D ratio 0.67. Five whorls, decoiling gradually. Almost flat-sided; first 4¼ whorls show very slight rounding of upper portion, then slight concavity, then very sharp periphery which overlies upper portion of lower whorl; sharp periphery changes on body whorl to rounded shoulder at aperture. First 3 whorls smooth. Fourth whorl partly smooth. Upper palatal surface of body whorl with 7 shallow spiral lirae crossing a multitude of very fine radial lines. On lower palatal surface, 13 flat spiral lines, not at all raised, cross many very fine radial lines. Even where shell is badly worn, traces of the spiral lines remain. Sculpture continues unchanged up to aperture. Aperture sub-circular, slightly compressed vertically, slightly appressed to penultimate whorl, slight extension at lower, inner quadrant. Parietal callus very thin. Umbilicus very wide, bounded by rim, open to nuclear whorl. D/U ratio 2.50. Thin, fragile, creamy white, with few remnants of thin, brown, deciduous periostracum. Operculum type C-2.

Collected by L. Price on November 20, 1965, at Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m, in light upland forest; Savaii, W. Samoa. FMNH 152991.

Range: Savaii, W. Samoa: northwest foothills and uplands. Altitude range 540–600 m.

Material: Station 33, up a survey track at 600 m elevation, approximately 8 km inland from Asau in heavy primary foothill forest (2 specimens, FMNH 152997); Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to 540 m elevation in light upland forest (1 specimen, (holotype) FMNH 152991).

Total: 3 specimens; 2 juvenile females, 1 juvenile male.

h. *Ostodes upolensis* (Mousson, 1865)

(Figures 24a, b; 25a; 26a, b)

Cyclophorus upolensis Mousson, 1865, Journ. de Conch., 13: 180, 181 – Upolu, Western Samoa.

Cyclophorus (*Ostodes*) *upolensis* (Mousson), 1869, Journ. de Conch., 17: 352 – Upolu.

Ostodes upolensis (Mousson), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 148 – Upolu; Kobelt, 1902, Das Tierreich, 16: 157 – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., 196: 12, 13; figs. 3 c, 28 e – Upolu: Latuafara, at 63.8 m elevation; Mt. Vaea; Lake Lanuto'o at 720 m elevation; Maldolelei, at 450 m elevation; Sinaele, at 420 m elevation; Tiavi, at 570–660 m elevation. Savaii: Salailua, at 300–600 m elevation.

Diagnosis: Shell broadly turbinate, small; height of adults 3.2–7.0 mm {4.9 mm}, diameter 2.8–8.6 mm {6.2 mm}, with 4⅛ to 5¼ whorls {4⅝}. Some have whorls with rounded shoulders, suture incised; others have smoothly sloping shoulders, very sharp keels, suture not incised. Nearly always wider than high; H/D ratio 0.66–1.14 {0.77}. Spire angle, 85°–110° {98°}. Umbilicus very wide, deep, nearly always sharply margined, but without a bordering rim; D/U ratio 1.62–3.77 {2.61}. Aperture round to subcircular, parietal callus not as thick as outer rim. Sculpture of strong spiral lirae and, in about half the adults seen, unobtrusive radial plicae. Body whorl with 5–8 {6.3} spiral lirae on upper palatal surface, crossing 15–25 {18.0} radial plicae; in about ¼ of adults seen, lower palatal surface showed 2–10 {6.0} spiral lirae only, often faint. Cream color, with thin, brown, deciduous periostracum. Opercular type, C-1.

Hypobranchial gland begins at left posterior margin of mantle cavity, runs across to slightly past mid-line, turns and runs forward only a short distance. Both anterior and posterior portions of moderate thickness. Male penis usually long-threaded, without sub-terminal bulb. Usually has both prostatic sac and "safety-valve." Female internal common duct very short, only 1/10 as long as bursa copulatrix is wide. Pallial common duct quite long; copulatory pore down from mantle line 3.5 pore diameters, distance from pore to entry into uterus equal to 6.5 X diameter of copulatory pore. Duct enters uterus via an L-shaped slit, the stem of the L at right-angles to long axis of uterus, the leg of the L pointing forward and having hypertrophied edges. Anus shows considerable hypertrophy of lips, especially on the upper margin. Vaginal orifice a slit on the medio-ventral aspect of uterus, its length approximately equal to uterine width at inner edge of orifice.

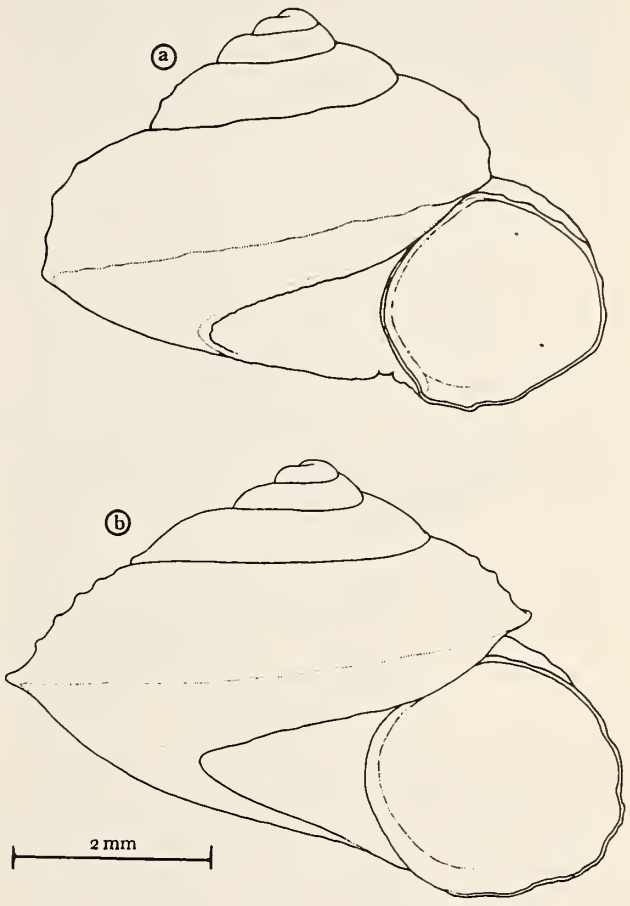


Figure 24

Ostodes upolensis

shell outline: a – "stepped form — b – "smooth" form

Comparative remarks: *Ostodes upolensis* is one of 3 small species in this genus. It occurs in 2 forms, the ordinary, or "stepped" form (Figure 24a) illustrated by Clench (1949: 11; fig. 3c), and a "smooth" form (Figure 24b). The "smooth" form was found only on Upolu, with juveniles at Station 2, and both adults and juveniles at Station 18. No "stepped" shells were found at those stations. Shells of the "smooth" form are slightly smaller than those of the "stepped" form and have a narrower umbilicus. Although males of both forms have long-threaded penes, those of the "smooth" form are very slightly longer, and the vaginal orifice of the females is very slightly smaller. The difference in shape of the 2 forms is caused by a difference in rate of decoiling. The rate is quite slow in the "smooth" form, with each whorl placed well up on the preceding one, and the peripheral carina is extended over the suture, thus producing a smoothly conical silhouette. In the "stepped" form, the rate of decoiling is much faster, each whorl being placed further down the whorl preceding it, and the peripheral carina being almost vertically below the next higher spiral lira, so that the shoulders are rounded. The narrower umbilicus in the smooth form is caused by a very pronounced insetting of the terminal portion of the body whorl under the penultimate whorl (see p. 196). Neither the difference in shape nor the very slight anatomical differences are considered sufficient to warrant separation of the 2 forms.

Neither form of *Ostodes upolensis* is likely to be confused with another of the small species, *O. cookei*. *Ostodes upolensis* is quite strongly sculptured, whereas *O. cookei* is the only species in the genus to present a smooth shell surface. The smooth form of *O. upolensis*, however, might be confused with *O. adjunctus*, from Tutuila. Clench's figure of *O. adjunctus* (Clench, 1949: 11, fig. 3b) shows a shell midway in shape between the two forms of *O.*

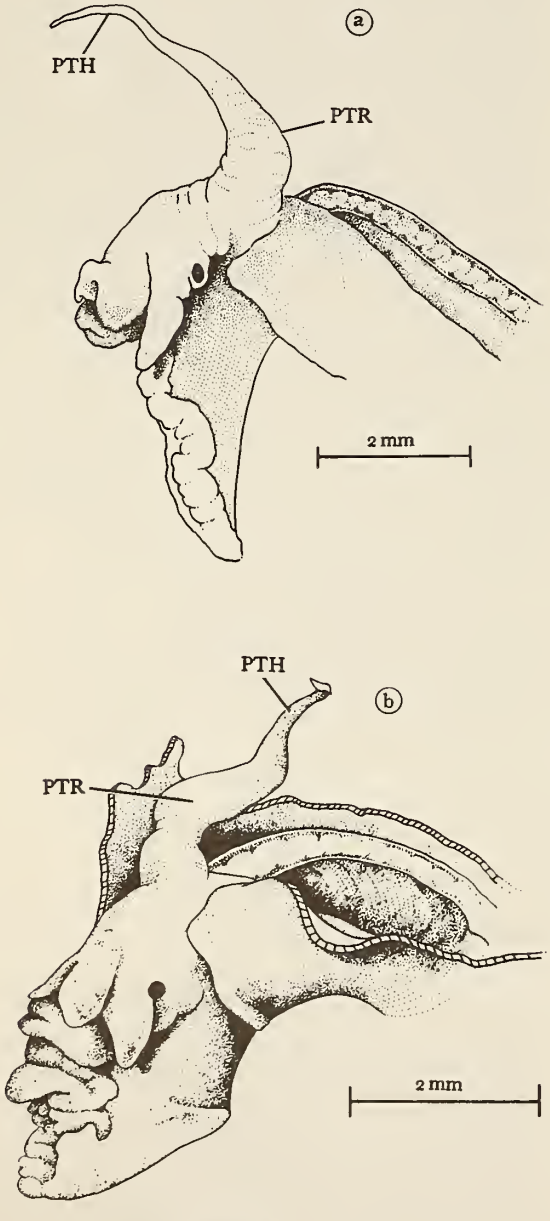


Figure 25

Males of (a) *Ostodes upolensis* and (b) *Ostodes adjunctus*
[for explanation of abbreviations see Appendix on foldout]

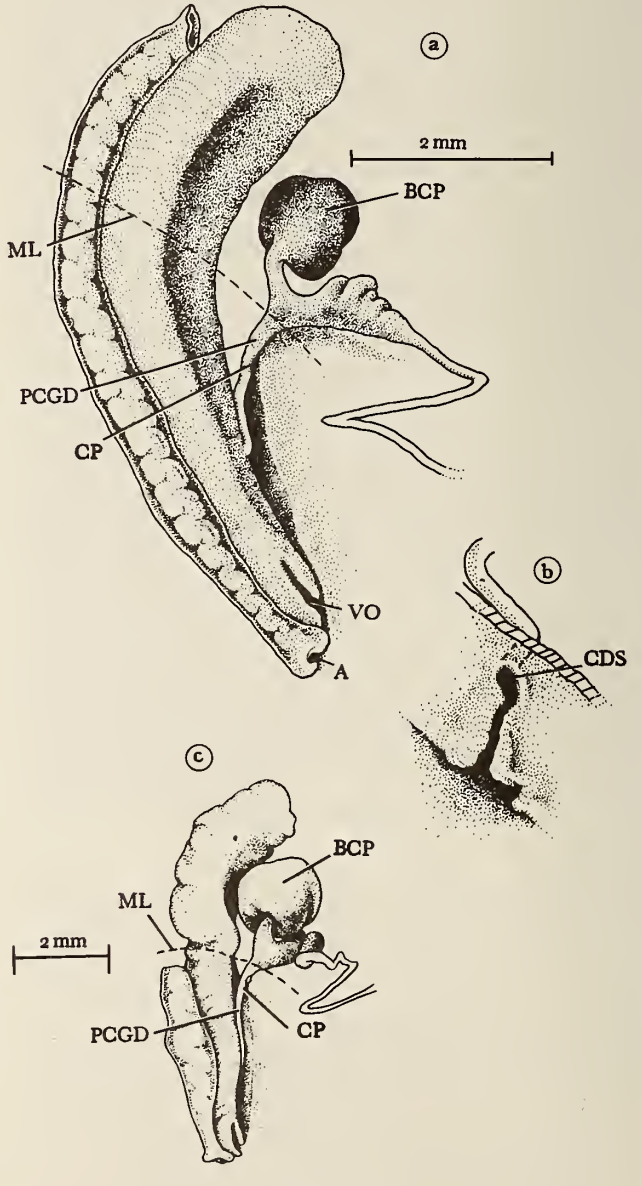


Figure 26

Female reproductive systems of *Ostodes upolensis* and *O. adjunctus*
a – *O. upolensis;* b – *O. upolensis*, entrance of common genital duct into uterus; c – *O. adjunctus*
[for explanation of abbreviations see Appendix on foldout]

upolensis. Mousson's original figure, however (Mousson, 1869: plt. 14, fig. 9) shows a very smoothly conical shell. The 40 shells of *O. adjunctus* available to me are also smoothly conical. Comparison of the "smooth" form of *O. upolensis* with the shells of *O. adjunctus* immediately shows the differences between the two. At the same or a lower whorl count, *O. adjunctus* is larger than *O. upolensis* (Figure 27). The umbilicus of *O. adjunctus* always has a bordering rim, whereas that of *O. upolensis* is rimless. *Ostodes adjunctus* has very strong spiral sculpture on the lower palatal surface, and is entirely lacking in radial sculpture, while in *O. upolensis* ventral sculpture is faint or absent and radials, though unobtrusive, are often present. *Ostodes adjunctus* is the only species of *Ostodes* in which shells that were otherwise clearly adult did not have the terminal portion of the body whorl indented beneath the penultimate whorl; in *O. upolensis*, especially in the smooth form, the indentation is very pronounced. Finally, fully half the shells of *O. adjunctus* examined had a bright red spire, a character never seen in *O. upolensis*.

Anatomically, the hypobranchial gland of *Ostodes upolensis* is much larger, especially the posterior portion, than that of *O. adjunctus*. Males of *O. adjunctus* entirely lack the prostatic sac and "safety-valve" so often present in *O. upolensis*. In the female, the pallial portion of the common genital duct is only half as long in *O. upolensis* as it is in *O. adjunctus*, and the vaginal orifice is only ⅔ as long.

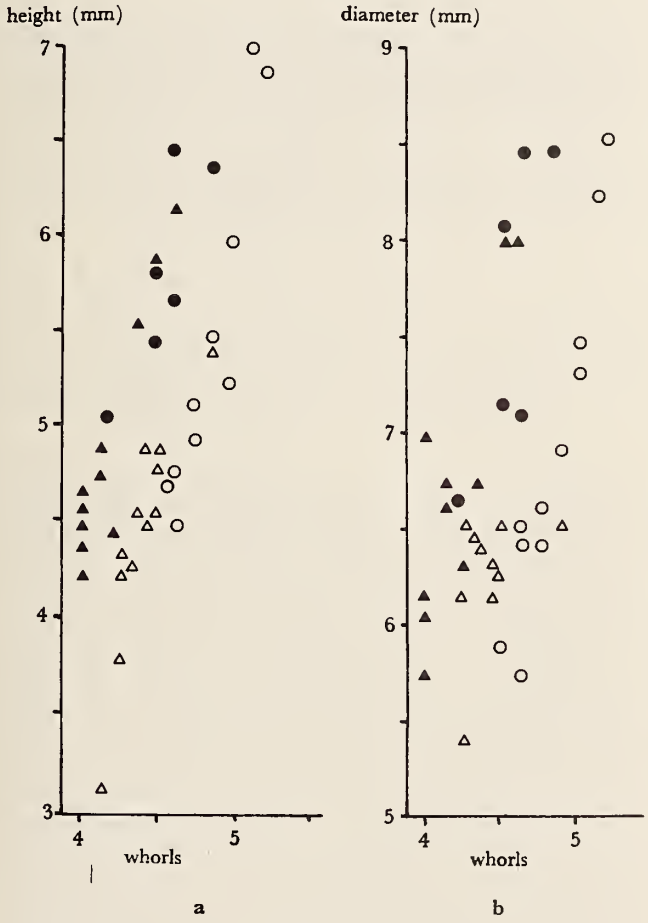


Figure 27

Relationship of whorl-count to size in *Ostodes adjunctus* and *O. upolensis* (both forms together)

a – height/whorls; b – diameter/whorls

▲ – *Ostodes adjunctus*, male ● – *O. adjunctus*, female
△ – *Ostodes upolensis*, male ○ – *O. upolensis*, female

Range: Upolu, Western Samoa: southern and northeastern lowlands, central foothills and uplands. Altitude range, 15–750 m.

Savaii, Western Samoa: southwestern lowlands at 150 m elevation.

Material: Savaii: Station 31, 2.2 km in from Salilua, 42 km west of Vailoa, at 150 m elevation, in heavy lowland forest (1 specimen, FMNH 152621); Upolu: Station 2, 1.2 km above Afiamalu seismographic station, on right of road, at 720 m elevation, in disturbed upland forest (4 specimens, FMNH 152710); Station 6, 1.6 km N of Mt. Siga'ele, at 555–570 m elevation, in a forest patch in a gully-pasture area (1 specimen, FMNH 152924); Station 8, 1.2 km above Afiamalu seismographic station, a wide area, including Station 2, on both sides of the road, at 720 m elevation, in mixed to good upland forest (5 specimens, FMNH 152686, 166212); Station 10, Togitogiga, two logging roads toward ocean at 15 m elevation in thinned lowland forest (3 specimens, FMNH 152953); Station 18, foot of Mt. Solaua, between 180–240 m elevation, under a large *Ficus* tree in a banana patch at edge of forest (45 specimens, FMNH 152850, 153026, 153093, 153104, 153169); Station 23, gully to foot of N side of Mt. Siga'ele, at 600–645 m elevation, in mixed to good foothill forest (18 specimens, FMNH 152605, 159170); Station 26, Afiamalu-Lake Lanuto'o track, at 735–750 m elevation, in good to excellent upland forest (1 specimen, FMNH 166211).

Totals: 77 specimens; 11 adult females, 11 adult males, 21 juvenile females, 24 juvenile males, 8 not sexed, 2 empty.

i. *Ostodes adjunctus* (Mousson, 1869)

(Figures 25b, 26c)

Cyclophorus (Ostodes) adjunctus Mousson, 1869, Journ. de Conch., 17: 351–352; plt. 14, fig. 9 – Tutuila.

Ostodes adjunctus (Mousson) Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 148 – Tutuila; Kobelt, 1902, Das Tierreich 16: 153 – Samoa (Tutuila); Clench, 1949, Bull. B. P. Bishop Mus., 196: 11–12; fig.

3b – Tutuila: Fagasa and nearby valley; Pago Pago at 60–150 m elevation; Amalau Bay, at 30 m elevation; NW slope on Mt. Pioa, at 180–240 m elevation; trail between Olofau and Amouli, at 90–120 m elevation; Aua-Afono Trail, at 300 m elevation; Amouli, half-way between Pago Pago and Alofau.

Diagnosis: Shell turbinate; height of adults 4.25–6.5 mm {5.25 mm}, diameter 5.75–8.5 mm {7.07 mm} with 4–4⅞ whorls {4¼}. Upper whorls have rounded shoulder, body whorl has angled shoulder, often with moderate keel. Suture incised. Only 4 adults of 17 examined showed any trace of indentation of terminal portion of body whorl, although the sculptural change marking the onset of maturity was very clear. Always wider than high; H/D ratio 0.67–0.83 {0.75}. Spire angle 80°–110° {92.5°}. Ventral surface flattened. Umbilicus wide and deep, margined with upstanding rim made by innermost ventral spiral lira; D/U ratio 2.50–3.89 {3.02}. Aperture almost square in juveniles to round in adults, appressed to whorl above. Parietal wall usually not as thick as outer lip. Early whorls smooth; body whorl with 5–6 strong spiral lirae on upper surface, 6–8 {6.5} spirals on ventral surface. Ventral spirals nearest umbilicus show the most relief; outer spirals less raised, may be just lines without relief; this may be due to wear. Shell has no radial sculptural elements of any kind except fine, close-set radial growth lines, which dominate shell surface at onset of maturity, when spiral lirae stop very abruptly. Color cream to dirty white except that slightly more than half the specimens seen had intense raspberry red spires for first 1¾–3¼ whorls {2¾}. Periostracum deciduous, pale yellow-brown, wears off raised spiral lirae quickly. Operculum types B, C-1.

Hypobranchial gland very small, extending only short distance to left of midline, and running forward hardly at all. Of 11 males examined, 2 had the penis to the right of the cephalic midline; the other 9 had the penis on the cephalic mid-line. Penis of some specimens seems unusually large in proportion to head. Penis usually long-threaded; no sub-terminal bulb, no prostatic sac, no "safety-valve." Prostate squared-off at anterior end, medial corner forming a flap under which vas deferens crosses to penial base. Vas deferens a short, straight tube, not long and convoluted. Female internal common duct very short, only 0.2 times diameter of bursa copulatrix. Pallial common duct quite long: copulatory pore down 2 pore diameters from mantle line, entrance of duct into uterus 16 pore-diameters below pore. Interior aspect of entrance of genital duct into uterus not seen. Anus points straight forward, with considerable hypertrophy all around edges. Vaginal orifice a long, narrow slit on medio-ventral aspect of uterus, its length 1.4 times diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes adjunctus* resembles *O. upolensis* more closely than it does any other species of *Ostodes;* see comparative remarks under *O. upolensis.* The sculptured shells of *O. adjunctus* could not possibly be confused with the smooth shells of *O. cookei,* and of course all the other species of *Ostodes* are too large to be confused with *O. adjunctus.*

Range: Tutuila, American Samoa: eastern portion of island: south-east coast and ridge of central mountains. Altitude range, 60–330 m.

Material: Station AS-1; steep hillside, banks of Visa Stream, 11 km E of Pago Pago at 60 m elevation (6 specimens, FMNH 181005/6). Station AS-2; steep ridge slope, at 90 m elevation, Siliataligalu Point, 11.7 km E of Pago Pago (27 specimens, FMNH 181011/N). Station AS-7; main ridge above Fagaitua, 18.4 km E of Pago Pago, at 210–240 m elevation (4 specimens, FMNH 181059/4). Station AS-9; crest of main ridge, left side of Aua-Afono track, 4.8 km E of Pago Pago, at 300–330 m elevation (4 specimens, FMNH 181078/4).

Totals: 40 specimens: 11 adult males, 5 adult females, 8 juvenile males, 12 juvenile females, 4 empty.

j. *Ostodes cookei* Clench, 1949

Ostodes cookei Clench, 1949, Bull. B. P. Bishop Mus., 196: 10–11; fig. 3 a – Upolu, Western Samoa: Tiavi, at 630 m elevation.

Diagnosis: Adult shell, turbinate, small, height 5.6 mm, diameter 7.5 mm, with 4⅞ whorls. Whorls with rounded shoulders, suture incised. Last ⅛ of body whorl inset under penultimate whorl. Wider than high, H/D ratio 0.74. Spire angle 110°. Aperture round, holostomatous, parietal wall as thick as outer lip. Umbilicus very wide, deep, open to nuclear whorl, D/U ratio 2.34, bounded by a rim that protrudes over the umbilicus but is not raised from the lower palatal surface of the shell. Shell cream color with very thin yellowish iridescent periostracum which is peeling off in spots and is missing from most of the spire and the last ⅜ of body whorl. Where periostracum is missing, shell shows pitting and wear. Shell appears entirely smooth to naked eye. Magnification of 16X reveals texture of many fine radial growth lines, crossed on upper palatal surface of body whorl only by 7 spiral lines, which are just lines, not raised at all from shell surface. Spiral lines stop and growth lines coarsen for last ⅛ whorl. Operculum not seen.

Anatomy not seen.

Comparative remarks: *Ostodes cookei* approaches the other two small *Ostodes, O. upolensis* and *O. adjunctus* in size and general configuration, but is smooth while the other two species are strongly sculptured. Although *O. tiara* and *O. garretti* may produce a secondarily smooth

surface due to wear, the difference in size makes confusion of either with *O. cookei* impossible.

Range: Tiavi, Upolu, Western Samoa, at 630 m elevation.

Material: Tiavi, Upolu, at 630 m elevation (1 specimen, MCZ 140504, paratype).

k. *Ostodes tiara* (Gould, 1848)

(Figures 7a, b; 8a, b)

Cyclostoma tiara, Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 204 – Upolu, Western Samoa; Gould, 1852, U. S. Explor. Exped., 12: 101; Gould, 1860, U. S. Explor. Exped., Atlas of Shells, plt. 8, figs. 116, 116 a.

Cyclophorus tiara (Gould), Gray, 1852, Cat. Phan., p. 58 – Upolu; Pfeiffer, 1852, Mon. Pneum., 1: 84 – Upolu; Reeve, 1862, Conch. Icon., XIII: sp. 76, plt. 16, fig. 76 – Upolu; Mousson, 1865, Journ. de Conch., 13: 179 – Upolu to 1,000 m elevation.

Cyclophorus (Ostodes) tiara (Gould), Mousson, 1869, Journ. de Conch., 17: 350 – Upolu.

Ostodes tiara (Gould), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 146–147 – Upolu; Kobelt, 1902, Das Tierreich, 16: 156, 157; Clench, 1949, Bull. B. P. Bishop Mus., 196: 17, 18; fig. 7b – Upolu, near Tiavi, at 630 m elevation.

Diagnosis: Shell broadly turbinate, very large; height of adults 12.5–16.2 mm {14.3 mm}, diameter 16.0–22.5 mm {18.2 mm}, with $4\frac{5}{8}$–$5\frac{5}{8}$ whorls {$4\frac{7}{8}$}. Whorls moderately carinate, suture not incised. Always wider than high; H/D ratio 0.71–0.86 {0.79}. Spire angle 100°–110° {107°}. Umbilicus usually wide, deep, margin smoothly rounded without bordering rim. D/U ratio 2.58–4.13 {3.37}. Aperture round, holostomatous, slightly appressed. to whorl above, parietal callus of adults almost as thick as outer rim of aperture. Sculpture usually worn off early whorls. Body whorl with 9–20 {15.4} spiral lirae on upper palatal surface, 5–11 {8.0} spiral cords on lower palatal surface. On juvenile shells, 14–23 {16.8} radial threads cross the spiral lirae on the upper palatal surface; radial threads may persist in a few adults, but most adults show no radial sculpture except fine growth lines. Color whitish. Periostracum thin, brown, adherent. Opercular types A-2 and C-3.

Hypobranchial gland very thick and heavy posteriorly; anterior portion narrow but dense nearly to front of mantle cavity. Males have two different types of penis, as discussed under anatomy of reproductive system of genus. Of 9 adult males measured, 6 had "smooth" penes – long threaded, without bulb (Figure 7a) while 2 had "bumpy" penes – short threaded, with "knuckle," "collar," and bulb (Figure 7b). (Of juvenile males examined, 4 had "smooth" penes, while 3 had "bumpy" penes.) Both types of penis can be associated with a "safety-valve," but a prostatic sac is rare in an animal with a "smooth" penis. Female internal common duct short, its length equal to only half the diameter of the bursa copulatrix. Pallial common duct very long; copulatory pore anterior to mantle line by twice its own diameter, and distal portion of duct equal to 26 times the diameter of the copulatory pore. Unlike all other species, *Ostodes tiara* has the entrance of the common duct into the uterus on the posterior (ventral) surface of that organ, near the lateral margin (all other species have the entrance on the medial margin of the

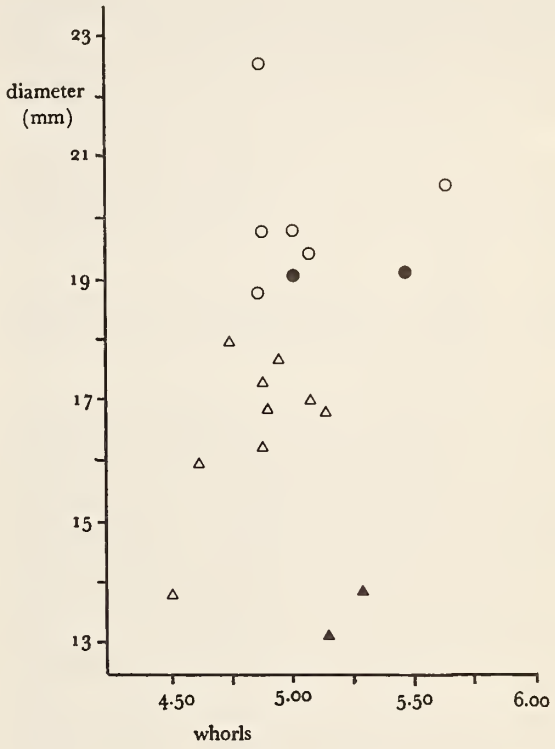


Figure 28

Relationship of whorl-count to diameter in *Ostodes tiara* and *Ostodes garretti*

△ – *Ostodes tiara*, male ○ – *Ostodes tiara*, female
▲ – *Ostodes garretti*, male ● – *Ostodes garretti*, female

uterus). Several attempts to expose the interior papilla of the common duct for drawing failed, and its shape and orientation remain unknown. Anus shows considerable hypertrophy of edges all around. Vaginal orifice a relatively small triangular slit, apex inward, its length only $\frac{1}{5}$ the diameter of the uterus at inner end of orifice.

Comparative remarks: *Ostodes tiara* is more similar to *O. garretti* than to any other species. For similarities and differences between the two, see comparative remarks under *O. garretti*.

Range: Upolu, Western Samoa: western, west-central, and north-eastern foothills; central uplands. Altitude range, 180–750 m.

Material: Upolu: Station 1, 1.6 km above Afiamalu seismographic station, to left of road, at 720 m elevation, in heavy upland forest to edge of sago-palm swamp (1 specimen, FMNH 152804); Station 2, 1.2 km above Afiamalu seismographic station, to right of road, at 720 m elevation, in disturbed upland forest (4 specimens, FMNH 152700, 153088); Station 8, 1.2 km above Afiamalu seismographic station, wide area on both sides of road, including Station 2, at 720 m elevation, in mixed to good upland forest (19 specimens, FMNH 152663, 152877); Station 16, SE peak Tafua-Upolu, at 480 m elevation, in undisturbed foothill forest (1 specimen, FMNH 152760); Station 18, foot of Mt. Solaua, between 180–240 m elevation, under a large *Ficus* tree in banana patch at edge of forest (1 specimen, FMNH 153175); Station 19, rim of Lake Lanuto'o crater, at 750 m elevation, in heavy upland forest (4 specimens, FMNH 152812, 152835); Station 26, Afiamalu-Lake Lanuto'o track, at 735–750 m elevation, in good to excellent upland forest (11 specimens, FMNH 152672, 152676, 152718, 166210); no locality given (1 specimen, FMNH 153819).

Totals: 42 specimens; 9 adult males, 10 adult females, 7 juvenile males, 5 juvenile females, 5 not sexed, 6 empty.

1. *Ostodes garretti* Clench, 1949

(Figures 7c; 8c, d)

Ostodes garretti Clench, 1949, Bull. B. P. Bishop Mus., 196: 18; fig. 7 c – Savaii: Siavao-Auola, at 150–600 m elevation; Salailua, from sea level to ± [sic] 780 m.

Diagnosis: Shell broadly turbinate, very large; height of adults 10.8–14.8 mm {12.5 mm}, diameter 13.2–19.2 mm {16.3 mm} with 5–5½ whorls {5¼}. Whorls carinate, suture only slightly incised. Always wider than high; H/D ratio 0.69–0.82 {0.78}. Spire angle 100°–115° {108°}. Umbilicus deep, wide; sometimes smoothly rounded, sometimes with bordering rim. D/U ratio 2.9–3.5 {3.19}. Aperture round, holostomatous, slightly appressed to whorl above, parietal callus of adults as thick as outer rim of aperture. Sculpture worn off early whorls. Body whorl with 7–15 {10.0} raised spiral cords on upper palatal surface, 11–13 {12.0} less prominent spiral cords on lower palatal surface. No radial sculpture except fine lines of growth. Color whitish, periostracum very thin, deciduous, brownish-yellow. Opercular types A-1, A-2, C-2.

Hypobranchial gland surprisingly small for so large a snail. Posterior portion very short, extending hardly at all to left of midline. Anterior portion runs well forward but is very narrow. Male penis with long thread without sub-terminal bulb; prostatic sac present; "safety-valve" may or may not be present. Female internal common duct very short, its length equal to only ¼ diameter of bursa copulatrix. Copulatory pore very close to mantle-line, but distal portion of pallial common duct very long – eight times diameter of copulatory pore. Entry of common duct into uterus is via a round elevated papilla inside medial aspect of uterus. Anus a simple tube without hypertrophy of lips, pointing forward. Vaginal orifice a long triangular slit, apex inward, its length equal to 2.6 times diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes garretti* is closely related to *O. tiara*. *Ostodes garretti* averages slightly smaller both in absolute measurement and in diameter for a given whorl count (Figure 28). Its umbilicus is very slightly wider in proportion to the diameter of the shell. The anatomical differences are considerably greater than those of the shells. *Ostodes garretti* has a much smaller hypobranchial gland. Its males have long-threaded penes without bulbs, whereas *O. tiara* males either have long-threaded penes without bulbs, or short-threaded, "bumpy" penes with bulbs. The greatest differences between the 2 species are found in the female reproductive system. Although both distal pallial common ducts are long, that of *O. tiara* is proportionately more than 3 times as long as that of *O. garretti*, and terminates on the ventral aspect of the uterus near the lateral margin, while *O. garretti*'s common duct enters the uterus in the usual way on the medial margin. Although *O. garretti* females have far less anal hypertrophy than do females of *O. tiara*, their vaginal orifices are proportionately more than 3 times as large as those of the latter species.

Range: Savaii, Western Samoa; northwest uplands.

Material: Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to 540 m elevation in light upland forest (8 specimens, FMNH 152986).

Totals: 8 specimens; 2 adult males, 2 adult females, 4 empty shells.

Remarks: *Ostodes garretti* has a more pronounced sexual dimorphism in size than any other member of the genus. At almost exactly the same whorl count, males averaged 21% shorter and 29% narrower than females.

C. The Generic Affinities of *Ostodes*

Tielecke's Poteriidae includes all of the helicoid cyclophorid genera from Central America, South America, the West Indies, and the South Pacific. Of the Pacific genera, *Ostodes* is the only Polynesian taxon, and it is restricted to Western and American Samoa (Clench, 1949: 3, 4). Names and distributions of the other nominate Pacific genera are: *Gassiesia* Clench, 1949 from New Caledonia and the Loyalty Islands; *Dublonia* Clench, 1949, *Paramia* Clench, 1949, and *Kondorhaphe* Clench, 1949 from the Caroline Islands; *Gonatorhaphe* Möllendorff, 1898 from the New Hebrides and Fiji; and *Fijiopoma* Clench, 1949 from Fiji. All of these genera were established on the basis of shell and opercular differences. Except for a few radular notes by Clench (1949: 48) and data in Solem (1959: 182–185; plt. 6, figs. 9, 10) on *Gonatorhaphe* genitalia, no anatomical information has been recorded. During this study, radulae from *Gassiesia* and *Gonatorhaphe* were examined with the aid of a scanning electron microscope (pp. 201-203), and their shells, anatomy, and opercula were examined rather briefly, as presented below. I have not seen any anatomical material from the Caroline Islands or from Fiji.

The Neotropical genera placed by Thompson (1969) in the subfamilies Neocyclotinae and Crocidopominae are included by Tielecke in the Poteriidae. Examples of a representative species from that group, *Mexcyclotus panamensis* (Da Costa, 1903), were dissected so that their reproductive systems could be compared with those of *Ostodes*. The results of those dissections are also presented below, along with a brief discussion of the shell and operculum. The radula of *Mexcyclotus* was not seen.

Specimens of too few genera have been dissected to permit any statements concerning phylogeny within the Poteriidae.

1. *Gonatorhaphe* spp.

Shell broadly turbinate, wider than high. Dorsal surface shows fine, close-set spiral lirae; some individuals also show broad, rounded, radial plicae. The ventral surface is smooth in the specimens from Espiritu Santo, and there is usually no umbilical rim. The spiral lirae are retained on the ventral surface of the specimens from Aoba, and the umbilicus has a rim. Aperture round, lip simple. Operculum with 2 layers. Lower layer smooth, shiny on under (attachment) side, thick centrally, diminishing to the vanishing point toward the edges. Upper layer of thin, transparent corneous material with an iridescent sheen for first 1.5–2.5 volutions, then becomes much thicker and heavily impregnated with calcium, the volutions lying immediately next to each other, their upper surfaces all on same plane. Result is a smooth-surfaced, thick, polygyrous, calcified operculum, with a small, non-calcified, depressed central area.

Radula similar to that of *Ostodes*.

Male reproductive system: Testis occupies entire volume of approximately first whorl; similar to that of *Ostodes* – branched digitiform alveoli, arranged in a single plane, feed into one collecting duct on the columellar side. Collecting duct runs forward as seminal vesicle. Prostatic lumen not seen. Anterior tip of prostate truncated, without sac or "safety-valve." Vas deferens a closed tube.

Penis quite variable. In specimens from Espiritu Santo, penis is standard short-thread type, without sub-terminal bulb; approximate thread-to-trunk ratio, 1/2.8. In specimens from Aoba, thread is shortened into a terminal appendage, triangular in cross-section and with sharp edges, usually found folded back acutely against trunk. Mean ratio, appendage to trunk, 1/3.8. Two specimens were seen in which the appendage was longer, with less acute edges, and looked more like a true thread; both had ratios of appendage to trunk of 1/2. One individual was seen which had both a closed vas deferens and an open groove on the posterior side of the penis. The groove did not run from prostate to penis, but began above penial base, ran up posterior side of penis, and ended just before distal end of penis folded over to become terminal appendage. The groove ran in a straight line, with the loosely coiled vas deferens running along beside it, plainly visible through the integument.

Female reproductive system: Ovary occupies columellar side of visceral mass for approximately first whorl. It is cylindrical in shape, composed of loose white granules, not macroscopically organized, enclosed in an encapsulating membrane which tapers anteriorly and becomes the oviduct.

Oviduct passes down columellar side of body almost to mantle line, then reflexes upon itself, passes upward, and makes another 180° turn into seminal receptacle. Oviduct throughout is thicker than the oviduct of *Ostodes,* and upon entry into seminal receptacle, it appears to be coiled, rather than folded, within the encapsulating membrane. Bursa copulatrix similar to that of *Ostodes,* its duct joining that from seminal receptacle in same way to become common genital duct. Common genital duct heavier than that of *Ostodes;* runs anteriorly along medial margin of uterus. Copulatory pore hidden by a flap of tissue extending from medial margin of uterus to floor of mantle cavity and forming a sort of roof over upper part of infra-uterine

channel, which is quite short. Entry of common duct into uterus is via an elevated papilla shaped like an inverted heart. Uterus bi-lobed, as in *Ostodes*. Vaginal orifice a triangular slit on medio-ventral aspect of uterus, just below anus, which shows moderate hypertrophy of upper lip.

Material: Baukaharijitoa above Dunduy, at 450 – 600 m elevation, Aoba, New Hebrides, FMNH 109423; Tasmalune, Espiritu Santo, New Hebrides, FMNH 109424.

2. *Gassiesia* sp.

Shell broadly turbinate, wider than high. Dorsal surface with spiral lirae, larger, wider-spaced, and more prominent than those of *Gonatorhaphe*. No radial plicae. Spirals continue on ventral surface, but umbilicus has no rim. Aperture round, lip simple. Operculum is similar to that of *Ostodes*: corneous, transparent with an iridescent sheen, polygyrous. Radula is enough different from that of *Ostodes* to be useful in differential diagnosis (pp. 202-203).

Male reproductive system: Testis occupies whole volume of approximately first whorl. Composed of branching, digitiform alveoli, arranged along outer aspect of collecting tubule on columellar side of whorl. Alveoli much finer, more closely packed, with fewer branches than in *Ostodes*. Collecting tubule becomes seminal vesicle, runs forward to enter prostate. Whole proximal tip of prostate turned under, with seminal vesicle entering at very tip. Prostatic lumen in turned-under portion is Y-shaped, stem of Y pointing medially, arms pointing laterally. Anterior to the turn in the main part of the prostate, the stem of the Y disappears, and the lumen is U-shaped, as in *Ostodes*. Anterior end of prostate shows small sac, but no "safety-valve." Vas deferens a closed tube. Penis long-threaded, thread/trunk ratio 1/1. In adult specimens, thread appears to have begun as a flattened ribbon which twisted upon itself repeatedly, so that its former edges show as two white lines, spiraling down from beginning of taper to very tip of thread. Thread of juveniles more rounded, lacks the white lines.

Female reproductive system: Ovary as in *Ostodes*: a tapering cylinder filled with loose white granules, enclosed in encapsulating membrane which continues forward as oviduct. Seminal receptacle as in *Ostodes*, with oviduct folded in one plane within encapsulating membrane. Bursa copulatrix very fragile, very thin-walled. Common duct as in *Ostodes*, but hidden for most of its length by a thin membrane running from medial aspect of uterus to mantle cavity floor, turning most of infra-uterine channel into a sort of tunnel. Copulatory pore not located. Uterus with two lobes as in *Ostodes*. Anus shows great hypertrophy of edges, especially of upper edge. Vaginal orifice a fairly large triangular slit, apex in, on medio-ventral aspect of the uterus.

Material: Station N.C. 15, near Thiem, N. E. New Caledonia. (juveniles, FMNH 159215): Station N.C. 28, W side of main range, ½ up, 6.4 km E of Ouegoa, N.E. New Caledonia. (adults, FMNH 159358). Both collected by Laurie Price, 1967.

3. *Mexcyclotus panamensis* (Da Costa, 1903)

(Figures 29, 30)

Shell broadly turbinate, wider than high. Surface smooth, showing only very fine radial growth lines. Periostracum adherent, thin, yellow to yellow-brown. Aperture round, lip simple. Operculum with 2 layers, as in *Gonatoraphe*, but of more complicated structure. Under layer smooth, shiny, thick in center, thinning towards rim, from which it protrudes as "cellophane edge." Upper layer corneous, transparent, with iridescent sheen for approximately first three volutions; then become heavily impregnated with calcium. Each subsequent volution is L-shaped, with the central half lying flat, the outer half standing up almost vertically from the surface. Flat half of calcified layer is overlaid by thin layer of iridescent, corneous material, extending upward from the under layer. Result is a small central corneous area, surrounded by upstanding, calcified lamellae, which are separated from each other by flat areas with a layer of calcium under a layer of corneous material. Environmental debris collects in interlamellar areas, where it seems to buttress the very brittle vertical lamellae against breakage.

Radula not seen.

Male reproductive system (Figure 29): Testis fills approximately first whorl of visceral hump. Internal structure not observed. Seminal vesicle runs down columellar side of body, enters prostate directly, without reflexing upon itself as it does in *Ostodes*.

Prostatic lumen approximately L or T shaped, the short arm or arms lying medio-dorsally, and the main part of the lumen running transversely. Prostate terminates in narrow, tapered tip, nearer to the base of the penis than in *Ostodes*. There is neither a prostatic sac nor any "safety-valve." Instead of a closed vas deferens, there is an open seminal groove, running from tip of prostate to base of penis. Penis on cephalic midline, well behind tentacles; short, thick, rugose, tapering abruptly into a slender neck surmounted by a narrowly-ovate, pointed terminal appendage. The seminal groove runs up the posterior sur-

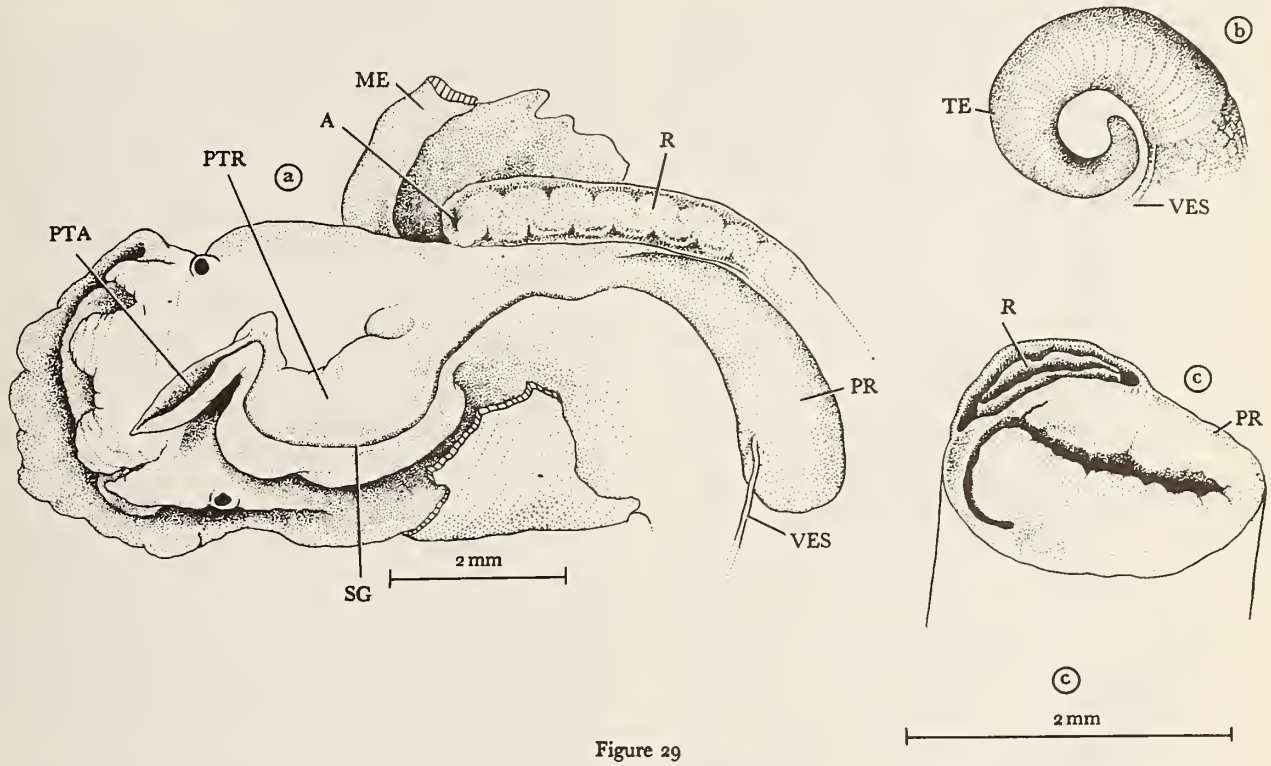


Figure 29

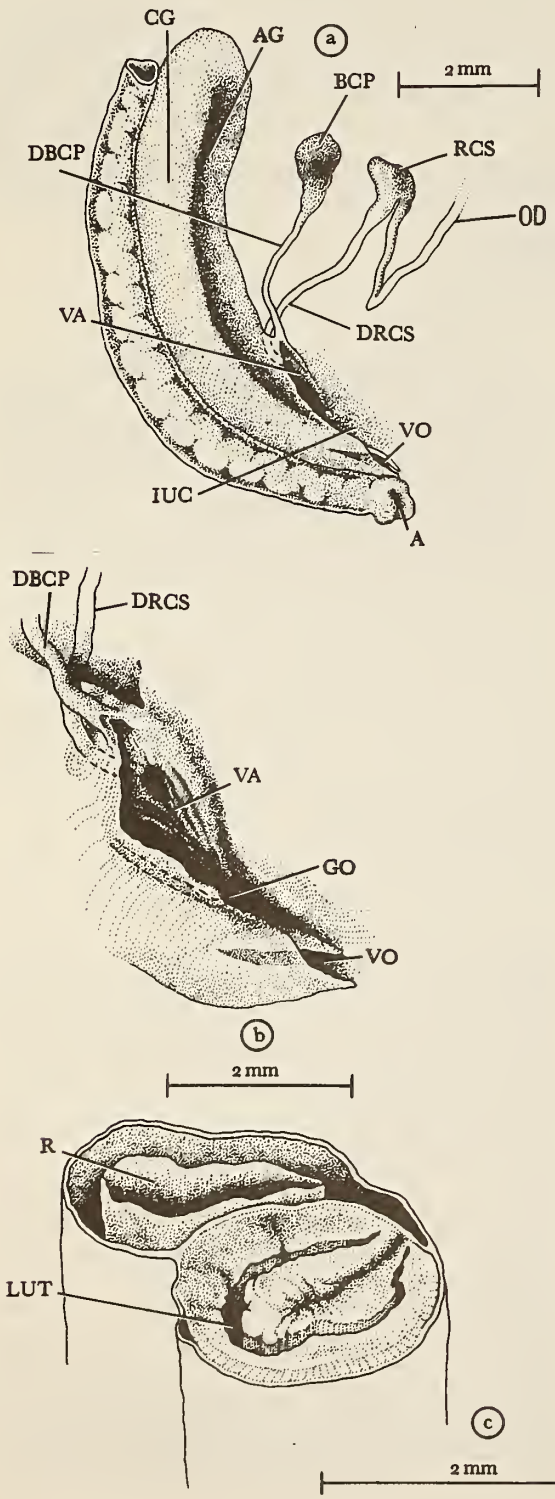
Mexcyclotus panamensis, male

a – viewed from above; b – testis; c – cross-section of prostate
[for explanation of abbreviations see Appendix on foldout]

face of the penis and across the neck, then opens into a deep, narrow, sharp-edged, spoon-like depression on the upper surface of the appendage. No important differences in proportion of terminal appendage to length of trunk were observed in the individuals examined.

Female reproductive system (Figure 30): Two forms of ovary have been observed in this species. One resembles the ovary of *Ostodes*: It occupies the columellar side of the visceral hump for approximately one whorl, and consists of white granular tissue, held together by an encapsulating membrane. It is shaped like a slender sausage, tapering at the ends, with the encapsulating membrane continuing anteriorly as the oviduct. Although ovaries with the second form occupy the same position, they are differently shaped: on the side away from the columella, 4 to 5 short, heavy, clavate alveoli protrude into the tissues of the digestive gland. The alveoli are arranged one behind the other, in a single row. Although one or two may be bifurcated near the outer end, the alveoli are not otherwise branched. This form of ovary seems to be made of the same sort of tissue as the smooth, sausage-like form; if the encapsulating membrane is torn, the white ovarian granules fall out loosely.

As in *Ostodes*, the oviduct runs down the columellar side of the body, becoming somewhat thickened and convoluted, then forms a seminal receptacle. A small sac-like structure, the bursa copulatrix, lies nearby, but is not directly connected to the seminal receptacle, and there is no common genital duct. Instead, both the receptacle and the bursa have long, slender ducts which open separately into a diamond-shaped vulval area, which is located at the proximal end of a very short infrauterine channel. The duct from the bursa copulatrix opens directly into the upper corner of the vulval area, while the duct from the seminal receptacle crosses behind the bursal duct and



makes a right-angled turn before entering the vulva distal to the entrance of the bursal duct.

The floor of the diamond-shaped area is thrown into deep, longitudinal rugae. Its medial margin is a prominent rounded ridge on the right side of the mantle-cavity floor; its lateral margin, and probably roof, is a thin flap of tissue extending medially from the lower portion of the medial aspect of the uterus. At the distal end of the vulvar diamond is a very small hole, hidden in and probably capable of being closed by the vulvar rugae, which opens into the uterus.

Two types of uterine structure have been observed. The first is similar to that seen in *Ostodes* (Figure 9c): there are two lobes, arranged in tandem, with the ventral lobe tan in color and of rather denser tissue than the dorsal lobe, which is creamy white and soft. The second type (Figure 30c) has a U-shaped lumen, which is continuous throughout the length of the organ. No bi-lobed structure is present, nor is there any differentiation in tissue texture or color in different parts of the uterus. There seems to be no correlation between type of ovary and type of uterus, both types of ovary having been found with each type of uterus. Although it is possible that the clavate ovary is a development of advancing age (the smooth types seen were smaller than the clavate examples), it is difficult to see how the uterine type could change during the lifetime of the individual.

The placement of the anal orifice and vaginal opening in *Mexcyclotus* is similar to the general arrangement in *Ostodes,* except that in the Central American snail, the hypertrophy of the anal orifice is horseshoe-shaped, open end up, and the vaginal orifice is partly obscured by a fold of tissue extending posteriorly and downward from the anterior tip of the upper vaginal lip.

Material: La Barca, Finca Lerida, at 1695 m elevation, Boquete, Chiriqui, Panama, FMNH 84611, 84621.

(← adjacent column)

Figure 30

Mexcyclotus panamensis, female

a – reproductive system, with bilobed uterus; b – greatly enlarged view of vulvar area; c – cross-section of uterus with U-shaped lumen

[for explanation of abbreviations see Appendix on foldout]

4. DISCUSSION

Gonatorhaphe and *Gassiesia* are obviously closely related to *Ostodes*. The shells of the 3 genera are very similar, using the same basic sculptural elements in varying combinations and with varying degrees of emphasis to produce shells of different appearance. The method is the same as that used between species in *Ostodes,* but the differences are greater between genera than between species.

In regard to operculum and radula, *Gassiesia* has a transparent, corneous operculum, very like *Ostodes'*. *Gassiesia*'s teeth, however, differ enough from those of *Ostodes* to be a useful diagnostic character. The radula of *Gonatorhaphe* is very similar to that of *Ostodes,* but the operculum, with its upper calcareous layer overlying the corneous under-layer, is quite different from the simple, corneous *Ostodes* operculum.

Although the anatomical differences between the 3 genera are greater than the differences between species of *Ostodes,* the differences all involve small details. In the male, *Gonatorhaphe*'s internal and prostatic arrangements are almost identical to those of *Ostodes,* the only differences being in the thread or terminal appendage of the penis. In *Gassiesia,* the testicular alveoli are smaller, more numerous, and less branched than are those of *Ostodes*. The upper end of the prostate is slightly different, and the penial thread is twisted. The 3 genera are alike, however, in having a closed vas deferens, and all have the penis on the dorsal mid-line of the head, behind the tentacles, the prescribed Poteriid position.

The situation is similar in the female systems. The questions of whether the oviduct folds or coils within the seminal receptacle; whether the wall of the bursa copulatrix is thick or thin; whether the infra-uterine channel is open or roofed-over, long or short – are all essentially minor points. All 3 genera have the oviduct, seminal receptacle, and bursa copulatrix opening into the uterus through a common duct – in accordance with Tielecke's definition of the Poteriidae.

Mexcyclotus is more strongly differentiated from *Ostodes* in shell, operculum, and anatomy, than *Gonatorhaphe* or *Gassiesia*. The shell is smooth and unsculptured; only *O. cookei* of the twelve species of *Ostodes* is smooth. *Mexcyclotus* has a heavily calcified operculum, in contrast to the corneous operculum of *Ostodes*.

In the male, the testis is smaller in *Mexcyclotus* than in *Ostodes;* the prostatic lumen is L- or T-shaped, rather than U-shaped; there is an open seminal groove rather than a closed vas deferens, and a spoon-like penial appendage rather than a smooth thread. Nevertheless, the penis is in the normal midcephalic position for the Poteriidae, and the cited differences do not seem to me to be sufficient cause for removing *Mexcyclotus* from Tielecke's family.

The differences between *Mexcyclotus* and *Ostodes* are much greater in the female reproductive system than in the male system. In *Ostodes,* there is a common duct serving the oviduct, seminal receptacle, and bursa copulatrix; in *Mexcyclotus,* the ovary and seminal receptacle enter the vulval diamond through one duct, while the bursa copulatrix enters through another. Can this be reconciled with Tielecke's definition of the family based on a single common duct? I think so. The basic requirement is that the products from the 3 organs enter the uterus together, and they do – they meet and mingle among the rugae of the vulval area and drain, together, through the single hole at the bottom of the vulva, into the uterus. This is a larger difference than exists between *Ostodes* and *Gassiesia* or *Gonatorhaphe,* but the functional pattern is the same.

For comparison, let us consider the situation in 2 of the other families. In the CYCLOPHORIDAE, either the oviduct, receptacle and bursa all enter the uterus separately (*Cyclophorus*), or the oviduct enters through the receptacle, and the bursa enters separately (*Spirostoma*). In the male, the penis is located behind the right tentacle, and there is an open sperm groove. In the MAIZANIIDAE, the penis has an open sperm groove and an accessory flagellum, and is located behind and at the same height as the right tentacle. The seminal receptacle drains into the oviduct, and the oviduct and bursa each have a very long, individual duct leading to the uterus. The differences between these families and the POTERIIDAE are much greater than the differences among the genera within the Poteriidae which I have examined. The differences I have seen between *Ostodes, Gonatorhaphe, Gassiesia,* and *Mexcyclotus* are certainly ample to differentiate them as genera, but they are not important enough to warrant separation at the family level.

VII. DESCRIPTIVE GEOGRAPHY

A. Location

Samoa consists of a group of islands at the westernmost extremity of Polynesia, lying between 11° and 15° S latitude, and longitudes 169° to 173° W. In Western Samoa, two small islands, Apolima and Manono, lie between two major islands, Upolu and Savaii. Savaii is the largest of the islands, being 50 km long by 28.8 km wide, with a maximum altitude of 1784 m. Upolu, lying southeast of Savaii, is also 50 km long, but only 17.3 km wide, reaching

an altitude of 1170 m. Tutuila, the largest island of American Samoa, lies SE of Upolu. Tutuila is much smaller than Upolu, having an area of only 133.1 km. Matafao Peak, on Tutuila, reaches an elevation of 643 m. Manua lies E of Tutuila, and is smaller; Rose Island lies E of Manua, and is smaller yet. Swain Island lies N and slightly W of Tutuila. The main Samoan islands are the tips of submerged volcanos, and volcanic activity has been observed as recently as 1911 (Schroth, 1971: 291).

B. Climate

The climate of Samoa is hot and wet. The southeast tradewinds flow along both sides of the high central longitudinal axis of the islands, dropping their moisture fairly evenly on the north and south sides. Only the northwest tips of the islands can be said to have an actual dry season. For the rest of the area, the mean annual rainfall ranges from 312½ cm to more than 500 cm. The rainfall increases with increasing altitude, the central uplands receiving more moisture than the coastal lowlands. The temperature falls an average of 1.5° C for every 300 m increase in altitude (Wright, 1963: 30), with the mean annual temperature ranging from 25.5° C in the coastal lowlands to 15.5 in the central highlands of Savaii.

C. Vegetation

The lowlands, from sea-level to about 225 m, used to be covered with a forest whose canopy reached 30–39 m high. Scattered remnants of this forest remain at present. The foothill forests, extending from approximately 225–540 m elevation, have a canopy height approximately the same as the lowland forests. They have more tree ferns, and the trunks of the canopy trees are adorned with mosses and lichens. The upland forests, from 540–1200 m, have still more tree ferns and ground ferns, more mosses and lichens, and an ample representation of monocotyledonous trees and epiphytes, including orchids and perching lilies. There is a 2½–7½ cm layer of leaf litter on the ground. An extensive list of the various species of trees, shrubs, and vines found in these classes of forest may be found in Wright (1963: 35–38).

VIII. ZOOGEOGRAPHY

A. Spatial

1. DISTRIBUTION on ISLANDS

During their field work in 1965, Dr. Solem and Mr. Price collected on both major islands of Western Samoa. The material available to me from Savaii came from a wide crescent including the western, southern, and eastern sections of the island. From Upolu, there was material from both north and south coasts, the easternmost tip, and the central and west-central uplands and foothills. The altitude range was from sea-level forest to 750 m. The material from Upolu contained individuals belonging to seven species: *Ostodes gassiesi, O. plicatus, O. **reticulatus**, O. savaii, O. **exasperatus**, O. upolensis,* and *O. tiara.* No examples of *O. cookei* were present in this collection. From Savaii came individuals belonging to six species: *O. gassiesi, O. savaii, O. **exasperatus**, O. garretti, O. **llanero**,* and *O. upolensis,* of which only one specimen was found. In 1975, Mr. Price collected on Tutuila, American Samoa, and sent back examples of *O. strigatus* and *O. adjunctus* from almost the whole length of the main central ridge, as well as the southern coast, taken at altitudes of 60 m to 390 m.

Four species of *Ostodes* from Western Samoa occur on both islands: *O. gassiesi, O. savaii, O. **exasperatus**,* and *O. upolensis. Ostodes plicatus, O. **reticulatus*** and *O. tiara* (as well as *O. cookei*) have been found only on Upolu, while *O. garretti* and *O. **llanero*** are known only from Savaii. Although *O. strigatus* has been reported from Western Samoa by older authors, it is now known only from Tutuila, as is *O. adjunctus.*

2. SYMPATRY

Over both islands of Western Samoa, the distributional pattern is one of sympatry. Of 30 collecting stations, only 9 yielded but one species. Of these 9 stations, 4 had only one or two specimens, and hence yield no significant data. In regard to the other 5 single-species stations, the 4 on Upolu yielded from 6 to 26 shells each, while Station 32, Savaii, gave 25 examples of *Ostodes savaii.* Each of the other 21 stations gave at least 2 species; while no station on Savaii had more than 3 species in residence, Stations 2 and 26 on Upolu each had 5 species, and Stations 8 and

18 each had 6 species. Station 18 was the best sampled and most intensively collected of any station visited.

In contrast, the situation on Tutuila seems to be one of complete allopatry. Stations 1, 2, 7, and 9, all on the eastern portion of the island, had only *Ostodes adjunctus*, while Stations 6, 10, 19, and 20, all on the western portion of the island, had only *O. strigatus*.

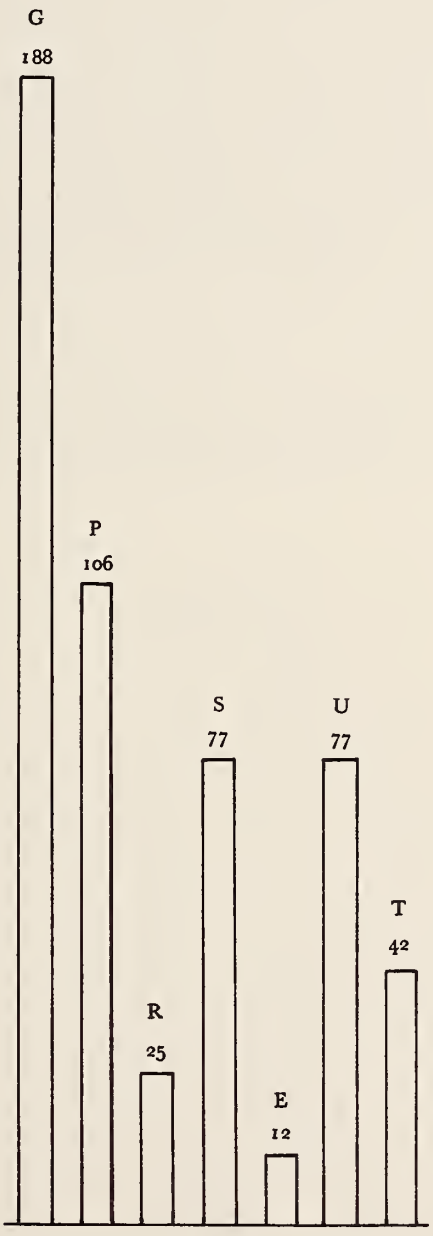
3. RELATIVE ABUNDANCE

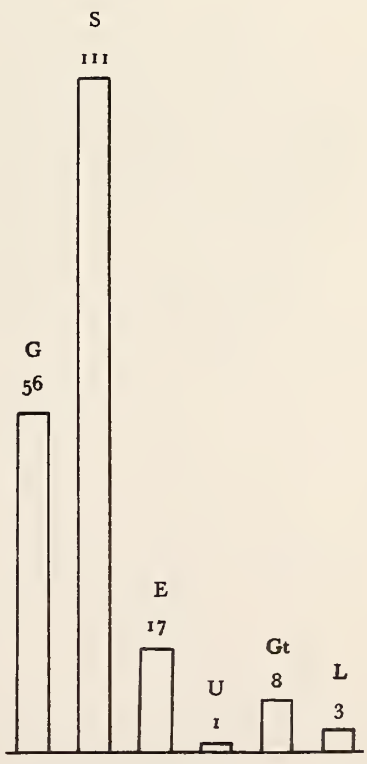
A total of 914 specimens were present in the material available to me. Of these, 526 came from Upolu, 195 were from Savaii, and 193 were from Tutuila. These numbers should not be taken as indicative of the true populations of the islands, however; Savaii is much larger than Upolu, but had less than half as many collecting stations, visited in a much shorter time. Tutuila was quite thoroughly collected. As stated above, 2 species were found on Tutuila, 7 species were found on Upolu, and 6 on Savaii,

Figure 31

Abundance of *Ostodes* in Western Samoa

E – *O. exasperatus*; G – *O. gassiesi*; Gt – *O. garretti*; L – *O. llanero*; P – *O. plicatus*; R – *O. reticulatus*; S – *O. savaii*; T – *O. tiara*; U – *O. upolensis*

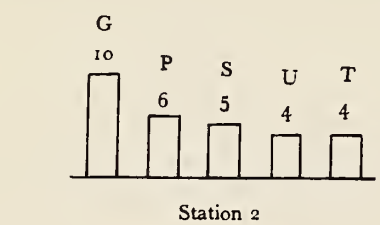




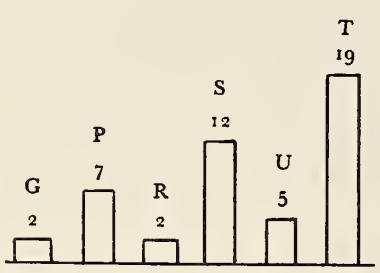
with 4 species being found on both Upolu and Savaii. These species were not collected in equal numbers, however. Taking all islands together, the most abundantly collected species is *Ostodes gassiesi,* with 244 specimens, followed by *O. savaii* (188), *O. strigatus* (153), and *O. plicatus* (106). The 3 species from Western Samoa were taken in different proportions on the two islands. On Upolu, 1.8 times as many specimens of *O. gassiesi* (188) were collected as of the next most abundant species, *O. plicatus* (106); *O. savaii* follows with 77 specimens. On Savaii, there are almost exactly twice as many *O. savaii* (111) as *O. gassiesi* (56), and *O. plicatus* does not occur at all. Figure 31 shows the varying abundance of the several species from both islands.

Within a given species in Western Samoa, the pattern of distribution seems to include both clustering and scattering. Each of the species which was found in any considerable number (more than 25 specimens) showed one to 4 stations having perhaps a dozen or more specimens, with the other individuals of the species divided, singly or in small groups, among a large number of different stations. For example, the 77 specimens of *Ostodes savaii* taken from Upolu came from 13 different stations, only 2 of which yielded 12 or more specimens, and 6 of which gave 3 shells (of this species) or less.

As mentioned above, 4 stations on Upolu had 5 or 6 species living together. The relative abundance of species



Station 2



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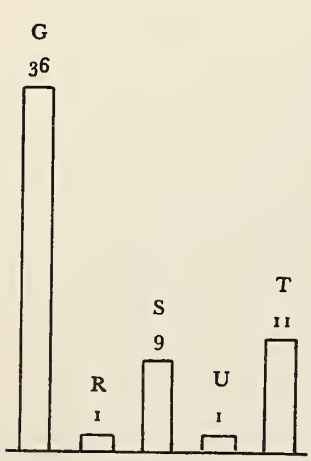
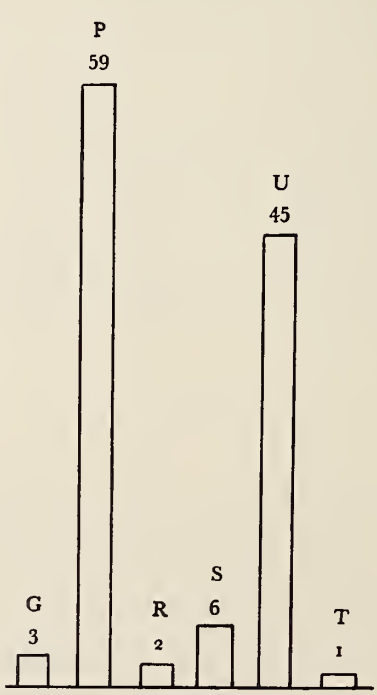


Station 26

Figure 32

Composition of sympatric populations of *Ostodes* on Upolu
[Species designations as in Figure 31]



Station 18

at these stations is shown in Figure 32. Station 2 (5 species, 29 individuals) is an area on the right side of a road, 1.2 km above Afiamalu seismographic station, at 720 m elevation, in disturbed upland forest. Station 8 (6 species, 47 individuals) includes Station 2 in a wider area of mixed to good upland forest on both sides of the road. The mean annual rainfall for these two stations is 437½–500 cm. Station 26 (5 species, 58 individuals) is on the Afiamalu-Lake Lanuto'o track, at 735–750 m elevation, in good to excellent upland forest. It receives more than 500 cm of rain annually. Station 18 is at the foot of Mt. Solaua, between 180 and 240 m elevation, under one large *Ficus* tree in a banana patch at the edge of the forest. The mean annual rainfall is 375–437½ cm. From this station, 116 individuals were obtained, belonging to 6 species. Dr. Solem has told me that this fig tree was an unusually rich collecting area, and was the only station at which he and Mr. Price made an attempt to "get everything."

It is interesting to note that at Stations 26 and 18, one or 2 species are dominant, with the other 4 represented by only a few individuals. At stations 2 and 8 the species are more evenly represented. The latter 2 stations represent larger sampled areas which probably included more microhabitats than the first 2 stations which were, respectively, a small remnant forest patch and a single huge fig tree.

B. Ecological

1. EFFECTS OF ENVIRONMENTAL DIFFERENCES

The principal environmental influence on land prosobranchs is moisture supply. Rainfall in Samoa is orographic, with higher altitudes receiving greater amounts of rainfall than lower elevations. Degree of moisture retention is controlled primarily by the vegetation cover, with heavy forest retaining moisture at ground level longer than open forest or cleared areas. *Ostodes* was collected only in areas with heavy tree cover (Solem, personal communication). Although specimens were taken in areas having different soil types, these stations also differed in rainfall regimes, and the relative importance of soil type and moisture supply could not be assessed. It is not known whether *Ostodes* obtains calcium through its plant food or by making use of free calcium in the soil.

The influence of a dry season on opercular type has already been mentioned (pp. 200-201). As stated there, specimens of *Ostodes savaii* from Station 32, Savaii (which receives a mean annual rainfall of 312.5–375 cm and has a more pronounced dry season than other stations) had thick opercula of a different type than individuals of the same species from areas which receive more rain, more evenly distributed through the year. That correlation did not hold for Upolu. Wet area-dry area differences have also been found in the shells and in the male anatomy, and these latter differences do hold for both Upolu and Savaii.

Specimens of *Ostodes savaii* from Station 32, Savaii, when compared with all other shells of the same species from the same island, prove to be smaller at the same whorl count (Figure 33). They are from 0.6 to 1.7 mm shorter, and up to 0.8 mm narrower. Additionally, although the males still have short-threaded penes, the threads are not quite as short as those of snails from more regularly moist areas. Males from Station 32 have a mean thread-to-trunk ratio of 1/3.2; short-threaded males from wetter areas have a mean ratio of 1/4.6 (Table 7). The

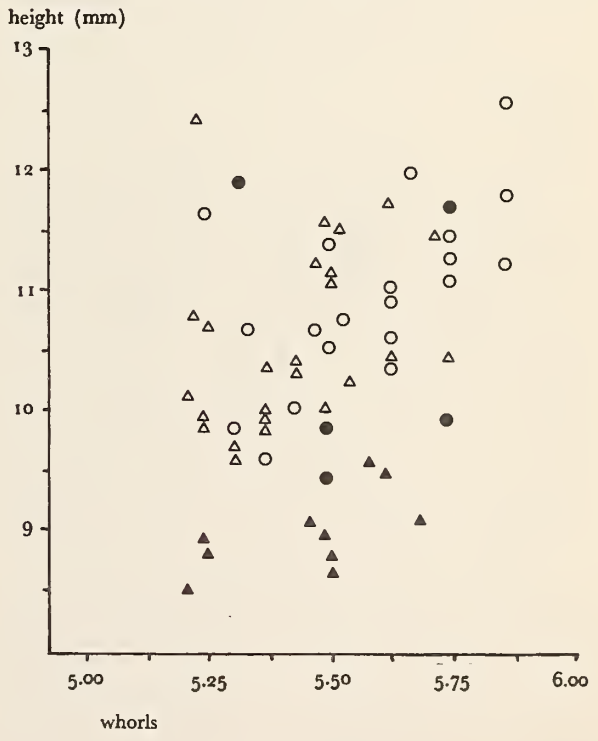


Figure 33

Effect of moisture on size in *Ostodes savaii* on the island of Savaii
▲ – males, Station 32 (dry area) ● – females, Station 32
△ – males, all other stations ○ – females, all other stations

Table 7

Effect of a Dry Season on Penial Thread-to-Trunk Ratio in Short-Threaded Males

Species	Island	Station	N	Range	Mean ± S.E.M.
Ostodes savaii	Savaii	32 (dry)	10	1/1.7 - 1/ 4.5	1/3.18 ± 0.28
		all other	19	1/1.7 - 1/10.0	1/4.38 ± 0.62
Ostodes gassiesi	Upolu	dry cluster	10	1/2.3 - 1/ 4.0	1/3.07 ± 0.17
		all other	26	1/1.7 - 1/10.0	1/4.11 ± 0.39

total length of the penis is the same in both wet and "dry" areas; only the proportion of thread to trunk changes with the climate.

On Upolu, there is a cluster of collection stations (Stations 5, 7, 14, 16, 17) which has the same climate as Station 32 on Savaii. Specimens of *Ostodes gassiesi* from the "dry cluster," when compared with individuals of the same species from areas without a dry season, tend to be smaller at the same whorl count (Figure 34). Males from these stations, like the "dry area" males from Savaii, have less-short penial threads (mean ratio 1/3) than do males from wetter areas (mean ratio 1/4) (Table 7).

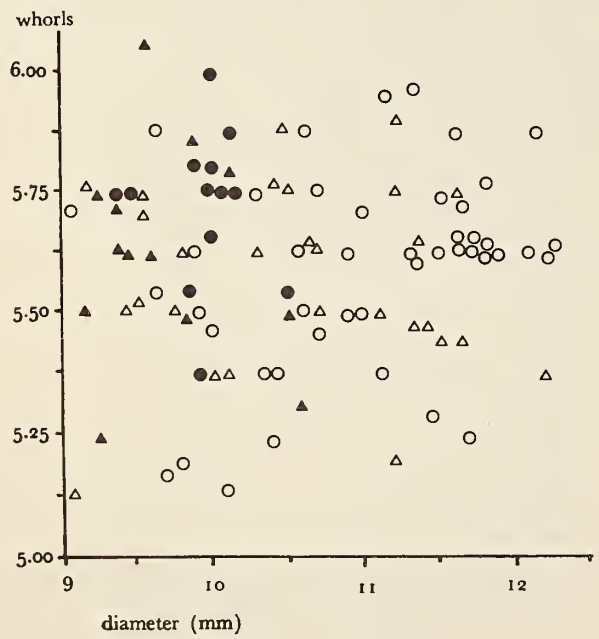


Figure 34

Effect of moisture on size in *Ostodes gassiesi* on Upolu

▲ – males from "dry cluster" ● – females from "dry cluster"
△ – males, all other stations ○ – females, all other stations

As important as the amount and regularity of rainfall, is what happens to the rain after it hits the ground. If a large amount falls, but runs off or evaporates quickly, it has much less value than a retained lesser amount. Therefore, the amount of vegetation – the density of the canopy and understory – is very important; the denser the cover, the more moisture will be retained, and the more favorable conditions will be for snails. This principle can be illustrated by a comparison of adult female *Ostodes gassiesi* from Station 2, Upolu, with adult female *O. gassiesi* from Station 19, Upolu. Both stations are in the upland forest, and both have the same type of climate, receiving from 437½–500 cm of rain per year, with no dry season. They differ, however, in that Station 19 has just average cover, while that of Station 2 is unusually lush. The effect of the increased cover is to make the moisture supply not necessarily more abundant, but less fluctuating in terms of ground-level near-saturation. The results are very apparent; at the same whorl-count, females from Station 2 are 9.3% taller and 8.7% wider than females from Station 19. Table 8 shows the results of a Student's *t* Test, which demonstrates that the size difference is really significant, and not just an artifact of collecting.

2. EFFECTS OF SYMPATRY

Sample size and distribution were such that comparisons of sympatric with allopatric populations were extremely difficult. In species with one good-sized allopatric population, individuals sympatric with other species were usually so scattered that meaningful statistical analysis was impossible. Indeed, there was only one instance in which I had both sympatric and allopatric populations of workable size: *Ostodes plicatus* from Upolu. *Ostodes plicatus* lives by itself at Station 39, and shares Station 18 with 5 other species. Comparison of 5 adults from Station 39 with 32 adults from Station 18 is shown in Figure 35; the